

A NEW SPECIES OF *LIMNOSCELIS*  
(AMPHIBIA, DIADECTOMORPHA) FROM THE  
LATE PENNSYLVANIAN SANGRE DE CRISTO  
FORMATION OF CENTRAL COLORADO

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ABSTRACT

A new species of diadectomorph limnoscelid, *Limnoscelis dynatis*, is based mainly on the greater part of an almost entirely disarticulated skeleton. It was collected from a previously described, highly fossiliferous quarry containing a wide variety of vertebrates of Late Pennsylvanian, probably Missourian, age in the Sangre de Cristo Formation of central Colorado. The disarticulated state of the materials has allowed a more detailed account of many aspects of the skeleton heretofore unknown in the closely related and only other known member of the genus, *L. paludis*. On the whole *L. dynatis* is more primitive than *L. paludis*.

INTRODUCTION

The family Limnoscelidae, best characterized by the species *Limnoscelis paludis*, has long been considered representative of the most primitive of "cotylosaurian" reptiles (Williston, 1911a; Romer, 1946; Baird and Carroll, 1967). More recently, however, Limnoscelidae has been reassigned (Heaton, 1980) to the amphibian order Diadectomorpha which also includes the families Tsejajidae and Diadectidae. Despite wide acceptance of this reclassification, the limnoscelids are still considered very close to the reptilian grade of organization, and, for this reason, have had a profound importance in studies on the origin and early evolution of reptiles. This has been greatly underscored in very recent cladistic studies (Gauthier et al., 1989; Panchen and Smithson, 1989) that unite the Diadectomorpha and amniotes as sister groups. More specifically, these analyses consider diadectomorphs as the sister taxon of synapsid mammal-like reptiles, and, among the diadectomorphs, *Limnoscelis* is viewed as being closest to the common ancestry with synapsids (Kemp, 1980).

*Limnoscelis paludis* was originally described by Williston (1911a, 1911b; 1912) on the basis of an essentially complete and articulated skeleton (the holotype YPM 811), as well as two other incomplete postcranial skeletons (MCZ 1947 and 1948, formerly YPM 819 and 809, respectively). Although the entire skeleton was available to Williston for study, his description was brief, and many postcranial elements were either not illustrated or crudely depicted. In a redescription, Romer (1946) focused mainly on the skull, and only it and the pelvis were reconstructed. Romer (1946) assessed *Limnoscelis* as a reptile, but with an anatomy so generalized as to be regarded a structural antecedent of later major groups of that class. Most

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recently, Fracasso (1983, 1987) has described in great detail not only the superficial structures of the skull, but most importantly the braincase. He concluded that diadectomorphs and *Seymouria* are primitive reptiles related most closely to pelycosaurs.

*Limnoscelis paludis* specimens have all been collected from the Late Pennsylvanian Cutler Formation of El Cobre Canyon in north-central New Mexico (Vaughn, 1963; Fracasso, 1980). A more precise determination of the age of the stratigraphic level from which the specimens were collected is somewhat controversial (Vaughn, 1963); the most recent assessments by Fracasso (1980) and Berman et al. (1987) are Missourian and Virgilian, respectively. The specimens of the new species of *Limnoscelis* described here were collected by Peter P. Vaughn of the University of California, Los Angeles, from a quarry in the Late Pennsylvanian Sangre de Cristo Formation of central Colorado near the town of Howard. Vaughn (1969, 1972) described from this quarry several vertebrates that included remains of a xenacanth shark and paleoniscoid fish, labyrinthodont amphibians, the aistopod amphibian *Coloraderpeton brilli* Vaughn (1969), the microsaur amphibian *Trihecaton howardinus* Vaughn (1972), the diadectomorph *Desmatodon hesperis* Vaughn (1969), and the pelycosaur reptiles *Edaphosaurus* aff. *E. raymondi* and *Edaphosaurus* cf. *E. ecorde*, and he estimated a Late Pennsylvanian, probably Missourian, age for the fauna. Several specimens collected from the quarry, representing both new and already known taxa, were not described by Vaughn, including (with minor exception) the almost totally disarticulated materials on which the *Limnoscelis* species described herein is based. Before the greater part of the *Limnoscelis* materials were excavated from the quarry during 1970–1973 and subsequently prepared, and before the presence of this genus was recognized, Vaughn (1969, fig. 1; 1972) mistakenly described two of its elements, a partial left dentary (incorrectly identified as a right palatine) and right premaxilla, as probably belonging to a large rhachitomous amphibian. In Vaughn's (1972) later paper on the fauna, an additional left premaxilla and portion of a left dentary were recognized as belonging to the same form, which was reinterpreted as possibly an anthracosaur, perhaps an embolomere.

Although the limnoscelid described here compares very closely with *L. paludis*, it exhibits numerous cranial and postcranial differences, enough to warrant its recognition as a distinct species. The disarticulated nature of the Colorado specimen permits a thorough description of the anatomy of this important vertebrate. Yet, an attempt to analyze the systematic relationships of *Limnoscelis* at this time would be premature, inasmuch as the authors have initiated a restudy of not only *L. paludis*, but of *Diadectes*, the best known member of Diadectidae, and *Tseajajia*, the sole representative of Tseajaiidae. It can be stated, however, that nothing has been revealed in this study that would significantly alter current understanding of the relationships of *Limnoscelis*, either among the diadectomorphs, or as a sister taxon to the synapsid mammals.

In 1987, all of the collections made by Peter P. Vaughn from the Permian and Pennsylvanian of southwestern United States and cataloged with the University of California, Los Angeles, vertebrate paleontology collections were permanently transferred to The Carnegie Museum of Natural History, Pittsburgh. The abbreviations used to refer to collection repositories are: CM, The Carnegie Museum of Natural History, Pittsburgh; MCZ, Museum of Comparative Anatomy, Harvard; UCLA VP, University of California, Los Angeles; and YPM, Yale Peabody Museum.



## SYSTEMATIC PALEONTOLOGY

## Class Amphibia

## Order Diadectomorpha

## Family Limnoscelidae Williston, 1911

Genus *Limnoscelis* Williston, 1911*Limnoscelis dynatis*, new species

*Holotype*.—CM 47653, disarticulated partial skull, lower jaw, and postcranial skeleton including: right premaxilla, right and anterior half of left maxillae; left posterolateral corner of skull roof table (portions of parietal, postparietal, tabular, and supratemporal); right parietal; right squamosal with probable adjoining portion of quadratojugal; left and partial right jugals; partial left quadratojugal; partial left pterygoid and fragment of transverse flange of probable right; quadrates; basiparasphenoid, otic-occipital, and sphenethmoid components of braincase; partial dentaries; partial probable right angular; 26 vertebrae that include complete or portions of two cervicals, eight dorsals, and 13 caudals of which there is only one isolated haemal arch; ribs include four complete or nearly complete cervicals, several incomplete dorsals, and two caudals, as well as fragments of many others; right clavicle; scapulocoracoids; right pelvis and disarticulated pubis and ischium of left; forelimbs include right humerus and partial left, right radius, and ulnae; hindlimbs include femora, right tibia and proximal and distal ends of left, and fibulae.

*Paratypes*.—CM 47651, associated partial left premaxilla, three parts of left dentary, right radius, partial left fibula, and three small bone fragments; CM 47652, associated left dentary and distal end of right tibia.

*Horizon and locality*.—Quarry in a 2–3 ft thick black shale in the Sangre de Cristo Formation, near the town of Howard in the Arkansas River valley, Fremont County, Colorado (see Vaughn 1969, 1972). The black shale unit was designated by Brill (1952) as part of “Interval 300” and lies about 1450 ft above the base of the approximately 2933 m Sangre de Cristo Formation section measured by him in NW $\frac{1}{4}$  NE $\frac{1}{4}$  SW $\frac{1}{4}$  sec. 22, T 49 N, R 10 E. On the basis of the associated fauna, Vaughn (1969, 1972) estimated a Late Pennsylvanian, probably Missourian, age.

*Diagnosis*.—*Limnoscelis dynatis* is distinguished from *L. paludis* in the following features: 1) rostral body of premaxilla not as massive and does not form ventral border of external naris; 2) absence of internasal bone; 3) jugal has well-developed postorbital process or bar, smooth, broadly concave external line of contact with squamosal on the dorsal margin of its posterior extension, and a straight margin along ventral free edge of skull; 4) toothed transverse flange of pterygoid narrowly subtriangular with laterally directed apex curved slightly posterolaterally, covered with small (diameter 0.3–0.8 mm) densely packed, blunt denticles except for single row of about eight larger (diameter about 2 mm), noninfolded teeth along the posterior margin; 5) marginal tooth counts of 17–20 maxillary and 23 or 24 dentary teeth greater, but overall sizes of teeth smaller except for first dentary tooth being much larger and nearly equal to the second and largest tooth of series; 6) scapular blade relatively shorter, with a greatest anteroposterior width near its summit exceeding the blade height above the glenoid by a few millimeters; 7) iliac blade is relatively shorter and wider, with a narrowest anteroposterior width across the neck slightly exceeding the blade height above the acetabulum, posterior process of the iliac blade ends at a level far short of the posterior end of ischium, and ridge-like external iliac shelf far less developed; 8)

pubis is roughly square in outline and shortened by a vertically truncated anterior margin, occupying only 38% of the puboischiadic plate length; 9) channel-like anterior extension of acetabulum about twice as long and reaches anterior margin of pubis; and 10) tibia longer than fibula, exceeding it by about 16%.

*Etymology.*—From the Greek *dynatos*, meaning strong, powerful, or able, referring to its probable role as a formidable predator.

#### DESCRIPTION

The *Limnoscelis dynatis* specimens were preserved disarticulated and, as such, there exists the potential problem of including with them isolated elements of other vertebrates of similar morphology either known or as yet not recognized from the same quarry. But, of the known members of the Howard, Colorado, quarry fauna (Vaughn, 1969, 1972), only isolated bones of the diadectomorph *Desmatodon* could be confused with *Limnoscelis*, a possibility all but eliminated for the cranial elements by Fracasso's (1983, 1987) description of the skull of *L. paludis*, which is quite distinct from that of *Desmatodon* (Vaughn, 1969, 1972). Identification of postcranial elements of *L. dynatis* was based not only on their similarity to those of *L. paludis* that were described by Williston (1911a, 1911b; 1912) and Romer (1946), but on the assumption that the noncranial elements of *Desmatodon* would have possessed the same features distinguishing them from *Limnoscelis* as those of its very close Lower Permian relative *Diadectes*. In addition, Vaughn's field and preliminary study notes of the Howard, Colorado, quarry fauna reveal that he carefully recorded the association of the excavated blocks that contained the majority of the holotypic elements of *L. dynatis*. Although the holotype was found scattered over about a nine sq ft area and associated with a few elements of *Desmatodon*, it clearly represented an association of matching elements of the major portion of a single skeleton.

#### *Cranial Skeleton*

The skull, braincase, and lower jaw are fragmentary, consisting mainly of isolated bones. The sculpturing pattern or ornamentation of the dermal bones of the skull roof and lower jaw is fairly consistent. The pattern is extremely fine, with a very subdued relief. At or near the center of ossification of an element, the sculpturing typically consists of ridges so tightly interwoven as to be separated by very small, porelike pits. The surface of the bone in this region often has the general appearance of being minutely pustular. More peripherally the ridges become longer and subparallel, forming an inosculate or anastomosing pattern. The ridges, and therefore their paralleling spaces, are typically extremely variable in width. At the margins of the elements the ridges are usually less interjoined and often appear to have a radiating pattern. Unless otherwise stated all of the elements described below, including postcranial, are assigned to the holotype CM 47653.

#### **Dermal Skull Roof**

*Premaxilla.*—The right premaxilla (Fig. 1A) is essentially complete except for possessing only the bases of the teeth. A fragmentary left premaxilla of the paratype CM 47651 (formerly UCLA VP 1737) is the same size, but does have a complete anterior tooth. Vaughn's (1969, fig. 1C; cataloged as UCLA VP 1700) description of the right premaxilla cited two teeth. When viewed medially, however, there is in the middle of what Vaughn interpreted as the base of the larger more anterior tooth a vertical, cutlike groove that marks the division between two closely ap-

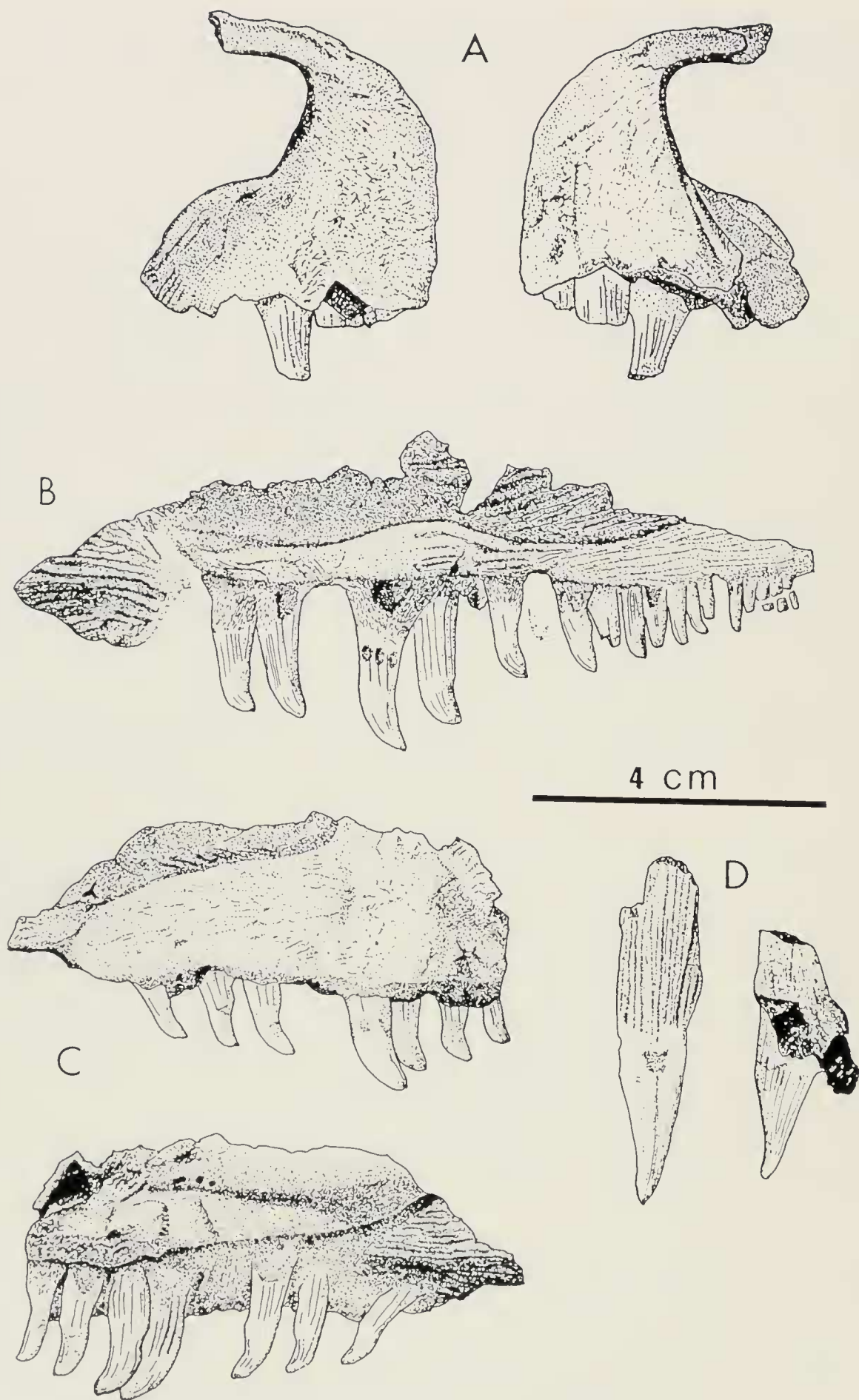


pressed teeth. In lateral view a small, displaced chip of bone from the ventrolateral margin of the premaxilla obscures the line of contact between the two teeth and allows the false appearance of a single, large tooth. It is possible, however, that the two teeth are preserved in a stage of one replacing the other and therefore occupy only one tooth socket. If correct, they should be counted as a single functional tooth.

The massive, blocklike rostral body of the premaxilla is narrowly subquadrangular in lateral view, with its posterior vertical border at approximately the level of the anterior margin of the external naris. A large maxillary flange extends posteriorly from the ventral half of the posterolateral margin of the rostral block. Its lateral sutural surface, marked by posteroventrally oriented, parallel striae, was overlapped by the premaxillary process of the maxilla and was essentially excluded from lateral exposure along the ventral border of the external naris. A much shorter vomerine flange extends posteriorly from the ventral half of the posteromedial margin of the rostral block. Its medial surface, marked by posteroventrally oriented parallel striae, is the articular surface for the vomer. Whereas the blocklike rostral body formed the anterior border of the external naris, the dorsal process formed approximately the anterior half of the dorsal margin. The dorsal process curves strongly posteriorly, suggesting that the middorsal surface of the snout did not rise noticeably posteriorly. The articulation of the dorsal process with the nasal was formed by a complex of interdigitating processes from both elements. There is no sign of an internasal bone along the midline union of the dorsal processes of the premaxillae as indicated by Fracasso's (1987) cranial reconstruction of *Limnoscelis paludis*. The midsagittal sutural plane of the rostral body is flat, coarsely rugose, and subtriangular in outline.

The premaxillary teeth are set in deep sockets; the anteriormost tooth is much larger than the following one or two. The only completely preserved premaxillary tooth is the anteriormost tooth in the left premaxilla (not figured). Its length in lateral view (much of the root is exposed in medial view) is 26 mm, and it is anteroposteriorly oval in cross-section, measuring 10 and 7 mm in anteroposterior and mediolateral dimensions, respectively. Nearly the basal third of the tooth, about 9 mm, remains constant in width, whereas the crown, approximately the distal 16 mm, tapers to a sharp point. The slightly concave posterior margin of the crown gives it the slightly curved appearance. A sharp, very narrow low ridge extends along the anteromedial and posterolateral lengths of the crown, passing through the crown tip. Loss of bone on the medial side of the premaxilla has exposed a large portion of the root. The root and much of the tooth base exhibit closely spaced, longitudinal, parallel grooves that are indicative of a labyrinthine structure, also evident on the large isolated teeth (Fig. 1D).

*Maxilla.*—The nearly complete right and the anterior half of the left maxilla are preserved (Fig. 1B, C). The right maxilla, exposed in medial view only, is missing a small amount of the dorsal lamina and almost surely a few millimeters of both its anterior and posterior ends. A portion of the underlapping suture for the lacrimal is preserved on the medial surface of the right maxilla, extending along the margin of dorsal lamina from the level of the anteriormost tooth to the largest or caniniform tooth. There is conspicuous lateral swelling of the maxilla at the level of the caniniform tooth. The medial surface is well preserved in both maxillae. An alveolar shelf extends nearly the full length of the maxilla, from its posterior end to the level of the first tooth. The shelf becomes more prominent anteriorly, but is most enlarged both medially and dorsally at its midpoint, the level of the caniniform tooth. Projecting anteriorly from the anterior end of the





alveolar shelf is a broad, diamond-shaped flange, the premaxillary process, that overlaps laterally the maxillary process of the premaxilla. The premaxillary process of the maxilla must have formed almost the entire ventral border of the external naris. The sutural surface of the process, which extends posteriorly to above the base of the first tooth, is marked coarsely by horizontal parallel ridges. The ventral half of the sutural surface curves laterally, so that it actually faces ventromedially. Fine striations on the medial face of the alveolar shelf from the posterior end of the maxilla to a level just posterior to the caniniform tooth mark the extent of its articulation with the palatine. A smooth, shallow, narrow groove, best seen in the partial left maxilla, extends along the dorsal margin of the alveolar shelf from its anterior end to the level of the caniniform tooth, ending just below a pair of foramina presumably for branches of the maxillary artery and the superior alveolar nerve.

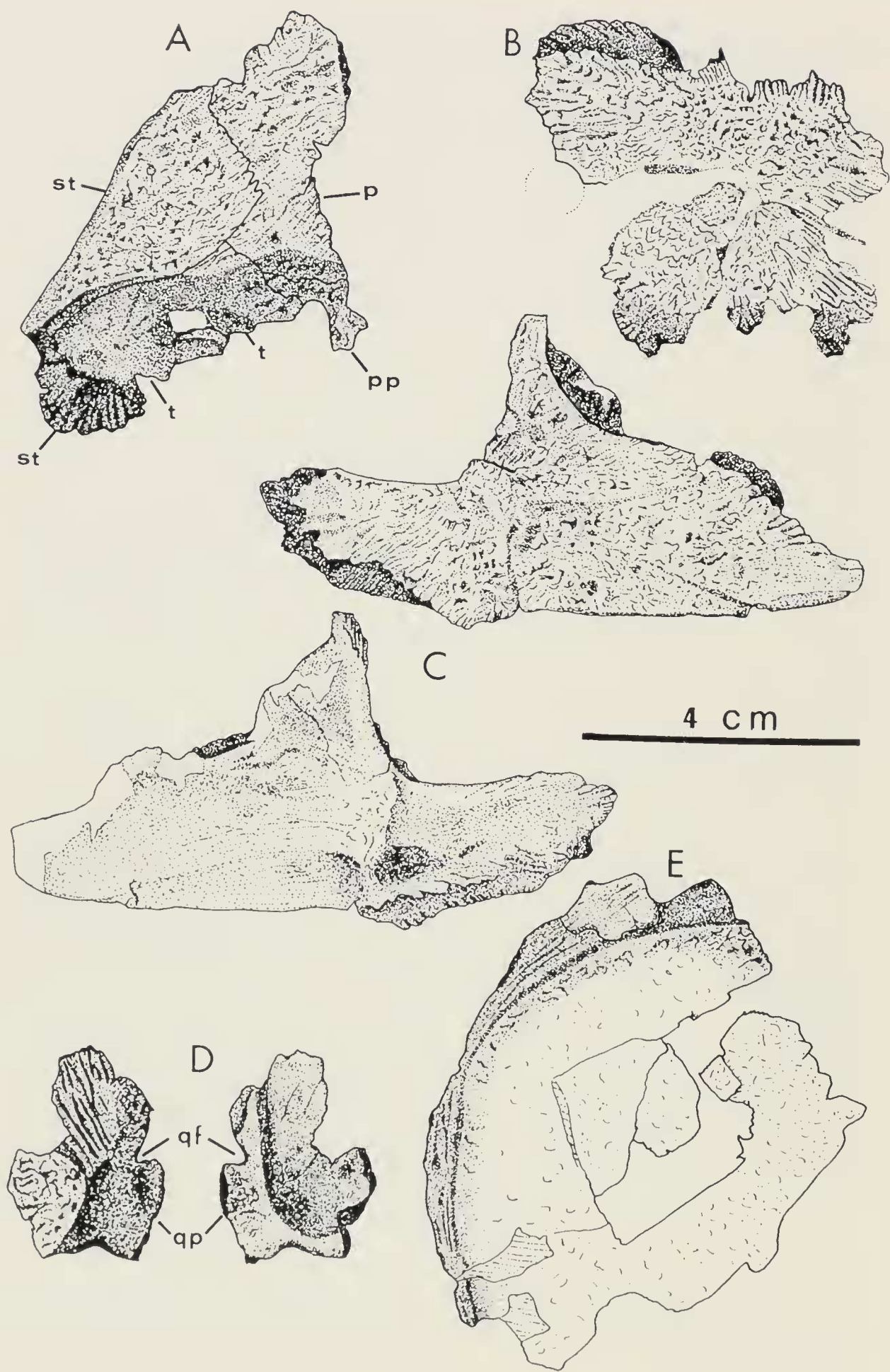
Although the maxillary teeth are set in rather deep sockets, they have a pleurodont-type attachment inasmuch as the lateral surface of the maxilla extends ventrally as a thin lip well below the alveolar shelf to support the dentition laterally. There appears to have been at least four teeth anterior and 17 posterior to the caniniform tooth, including empty sockets, for a minimum total of 22 maxillary teeth. The first four precaniniform teeth show a slight decrease in size anteriorly. The first postcaniniform tooth is noticeably larger than the last precaniniform tooth, and there is a general size decrease in the series posteriorly. The teeth are, for the most part, anteroposteriorly oval in cross-section. The basal halves, or bases, are constant in width, whereas the distal halves of the teeth, or crowns, taper to a point and are modestly curved posteriorly. A sharp, very narrow, low ridge extends the entire fore and aft lengths of the crown, passing through the tip of the crown. On the caniniform tooth the ridge is oriented along an anteroposterior vertical plane, whereas in the pre- and postcaniniform teeth the ridge runs from the anteromedial to the posterolateral margin of the crown. The crown is slightly concave on its posteromedial surface and is slightly angled in that direction so as to give it a hooked appearance.

*Parietal.*—Though only about the lateral third of the left parietal is preserved, it is articulated with portions of the postparietal, tabular, and supratemporal (Fig. 2A). A fragment containing a portion of the parietal foramen rim probably belongs to the left parietal. The isolated right parietal (Fig. 2B) is nearly complete except for portions of its midline contact with its mate, and its marginal contacts with other neighboring bones can, for the most part, be determined. The parietal underlapped the frontal and postfrontal with a superficial serrate sutural contact. The lateral margins of both parietals appear to be intact and indicate that the anterior half extended beyond the posterior half as the lateral parietal lappet. The lateral margin of the lappet trends anteromedially and undoubtedly contacted the postorbital in what appears to have been a serrate, abutment suture. Posterior to the lateral lappet the lateral margin of the parietal is deeply incised by an angular entrant of the supratemporal that dorsally overlaps it in an interdigitating suture. The posterior margin of the parietal is incomplete. There are three tablike flanges,

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Fig. 1.—Skull roof bones of *Limnoscelis dynatis*, holotype, CM 47653. A, lateral and medial views of right premaxilla; B, medial view of right maxilla; C, lateral and medial views of anterior half of left maxilla; D, isolated teeth.





measuring 4 to 8 mm in anteroposterior width, that project posteriorly from a level about 1 mm below the surface of the main body of the right element. The flanges were obviously part of a continuous posterior border of the parietal that was depressed ventrally in an almost steplike manner below the otherwise generally flat dorsal surface. A small portion of the far lateral end of the flange is preserved in the left parietal. The flange, which is less intensely sculptured than the rest of the dorsal surface, probably represents, as described by Romer (1946) for *Limnoscelis paludis*, that portion of the skull roof that slopes moderately posteroventrally from the more or less horizontal table to the nearly vertical occipital plate. The transverse posterior margin of the posteroventral sloping flange of the parietal contacts the postparietal along most of its medial length and the tabular for a short distance laterally. Here the parietal-tabular contact is continued for a short distance anterolaterally on the more dorsal surface of the skull table to its juncture with the supratemporal. A parietal-tabular contact precludes a supratemporal-postparietal contact. Though most of the medial margin of the right parietal is not preserved, the presence of a portion of the parietal foramen indicates that only a very narrow strip is missing. The parietal foramen, positioned slightly anterior to the midlength of the midline suture of the parietals, may have been as much as 7 or 8 mm in diameter.

*Postparietal.*—Only a small portion of the anterolateral corner of the left postparietal is preserved (Fig. 2A); it appears to wedge laterally between the parietal and tabular in the articulated posterolateral portion of the skull roof table. It is not possible to determine whether the postparietal was single or paired, but it was confined to the posterior portion of skull table sloping posteroventrally to the occiput. As in the posteroventrally sloping flange of the parietal, the sculpturing of the postparietal is less intense than that of the dorsal surface of the skull table.

*Tabular.*—An incomplete left tabular, preserved in the articulated posterolateral portion of the skull roof table (Fig. 2A), is bordered anterolaterally by the supratemporal and anteromedially by the parietal and postparietal. Its posteroventral occipital portion is missing and presumably would have included a square, dorsomedial plate that articulated with the supraoccipital and paroccipital process, and a long rectangular plate that extended ventrolaterally along the posterior margin of the cheek to over half the distance to the jaw joint (Huene, 1956; Fracasso, 1983, 1987). The preserved portion of the tabular is smooth and slopes posteroventrally at approximately the same angle as the postparietal except for a small triangular sculptured area that contributes to the skull table at the supratemporal-parietal juncture.

*Supratemporal.*—Only the left supratemporal is present and is part of the articulated posterolateral portion of the skull roof table (Fig. 2A), where it contacts the parietal medially and the tabular posteriorly. Its external sculptured surface is subtriangular in outline, forming a posterolaterally directed, hornlike process at the corner of the dorsal skull table. The anteromedial border of the supratemporal deeply encroaches into the posterolateral border of the parietal in a strongly

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Fig. 2.—Skull roof bones of *Limnoscelis dynatis*, holotype, CM 47653. A, dorsal view of left posterolateral corner of skull table containing portions of parietal (p), postparietal (pp), supratemporal (st), and tabular (t); B, right parietal (anterior toward top of page); C, lateral and medial views of left jugal; D, lateral and medial views of partial left quadratojugal; E, partial right squamosal with probably small adjoining portion of quadratojugal. Abbreviations: qf, quadrate foramen; qp, quadrate process.

interdigitating suture. The posteromedial border of the supratemporal, extending to the end of the hornlike process, contacts the tabular in a smooth, slightly sinuous external suture, then apparently underlaps it for a considerable distance. It appears that the posteroventral portion of this suturally underlapping flange of the supratemporal has been exposed along the ventrolateral margin of the incomplete tabular. The exposed sutural surface of the supratemporal exhibits what appears to be a series of parallel grooves and ridges. The short anterior border of the supratemporal appears to be complete and undoubtedly contacted the postorbital. The lateral border of the supratemporal is smooth and nearly straight in dorsal view, but in lateral view is slightly concave, with a narrow, ventrally facing sutural surface for the dorsal margin of the squamosal.

*Squamosal.*—The greater portion of the probable right squamosal is exposed in lateral view (Fig. 2E). Its posteroventral area very likely includes a portion of the adjoining quadratojugal. In *Limnoscelis paludis* the suture between these two elements apparently became completely fused near the posterior margin of the cheek and is impossible to trace (Romer, 1946; Fracasso, 1983). The combined elements form most of the cheek. In lateral view their flat external surface is subcircular in outline, with the dorsal and posterodorsal margin forming a smooth convex arc. Along this arclike border there is a well-formed, but incompletely preserved, medially directed sutural flange. The anterodorsal half or more of the medial flange, undoubtedly formed by the squamosal, is directed dorsomedially and would have suturally underlapped the lateral margins of the postorbital and supratemporal. This suture is the “zone of structural weakness” between the dorsal table and the lateral cheek described by Romer (1946:152–153), who notes that it is not restricted to *L. paludis*, but is present in such moderately advanced amniotes as the pelycosaur. The posteroventral half or less of the medial flange of the combined squamosal and quadratojugal most likely originates mainly from the latter element. It is directed mainly posteromedially and probably suturally underlapped the long ventrolateral extension of the tabular along the occipital margin of the cheek as in *L. paludis* (Fracasso, 1983).

The incomplete medial flange of the combined squamosal-quadratojugal varies in width from about 3 to 10 mm, and is widest at its anterior end. The character and intensity of the sculpturing of its sutural surface for the dorsal skull table also varies. At the anterodorsal end of the flange the anteroposteriorly oriented striations and ridges of the scar are fewer and much more subdued than at the posteroventral end. The identification of the combined squamosal-quadratojugal in Fig. 2E as coming from the right side of the skull is based, in part, on the match between the sculpturing pattern of the sutural scar on its medial flange with that of the partial flange of the incomplete left quadratojugal described below. In addition, the sculpturing pattern on the lateral surface of the squamosal-quadratojugal adjacent to the posteroventral end of the medial flange matches that of the fragmentary left quadratojugal in being minutely nodularlike with very short irregular ridges surrounding very small, irregular pits. Elsewhere on the squamosal-quadratojugal the pits and ridges of the sculpturing are longer and subparallel.

*Jugal.*—Both jugals are present; whereas much of the right is missing, the left (Fig. 2C) is essentially complete. The jugal is triradiate, and its external surface is very slightly convex in horizontal section. A broad anterior extension forms much of the slightly concave, ventral orbital margin, probably extending anteriorly a short distance beyond the midlength of the orbit. The anterior extension ends in a posteroventrally inclined sutural border that underlapped the maxilla and



lacrimal. A narrow, dorsal, postorbital process forms much of the posterior border of the orbit. A small sutural scar on the medial surface of the distal end of the process marks its contact with the postorbital. The very broad posterior extension of the jugal had an underlapping contact with the squamosal and quadratojugal along its posteroventrally sloping upper border. The portion of the sutural margin along the angle formed between the postorbital bar and the anterior portion of the posterior extension is steplike in transverse section, with a broadly concave external line of contact for the squamosal. The more steeply inclined posterior half of the posteroventrally sloping sutural border contacted the quadratojugal. The free border of the jugal along the ventral margin of the skull is straight.

The medial surface of the jugal is fairly smooth except just beneath the posteroventral corner of the orbit, where there is a prominent medial process for articulation with the ectopterygoid and palatine. There is also a pronounced medial thickening along the orbital rim.

*Quadratojugal.*—Part of the quadratojugal is preserved with the right squamosal described above. A small, isolated portion of the left quadratojugal also occurs (Fig. 2D). This fragment came from the posteroventral corner of the skull and includes not only a small portion exposed on the lateral cheek, but a medially directed portion that is visible in occipital view. The small, preserved triangular sculptured area that represents the posteroventral corner of the cheek has a strongly convex, smoothly finished posterior border that is slightly elevated over the smooth medially bordering bone. Dorsal to the sculptured surface of the cheek is a portion of the quadratojugal's medial sutural flange that underlapped the distal end of the ventrolateral occipital extension of the tabular. The preserved portion of the medial sutural flange is essentially vertically oriented, with its posterior facing external sutural surface exhibiting strong ventromedially oriented striations and ridges. Ventral to the medial sutural flange a smooth, subrectangular quadrate process extends medially from the posterior margin of the sculptured cheek portion. The process, which appears to be complete, is greatly thickened in parasagittal section, and thins to a smoothly rounded ventral edge. The medial surface of the quadrate process had a wide contact with the lateral margin of the quadrate. The ventral margin of the quadrate process slopes slightly ventromedially and would have been visible in lateral. A smooth notch, forming the lateral margin of the quadrate foramen, lies between the dorsomedial corner of the quadrate process and the ventromedial edge of the medial sutural flange. The internal surface of the incomplete left quadratojugal is essentially smooth, with a deep, almost hemispherical pocket lateral to the quadrate process.

### Palatal Complex

*Pterygoid.*—The pterygoids are the only bones of the dermal palate preserved. They are represented almost exclusively by the partial left exposed in ventral view on a small block of matrix (Fig. 3A). It consists of the central, toothed, transverse flange and basal articular area, and the posterior quadrate ramus; the anterior palatal ramus is absent. All that remains of the right pterygoid is a large fragment of the toothed transverse flange. The transverse flange consists mainly of a tooth ridge that is narrowly subtriangular, with the laterally directed apex curving slightly posterolaterally. A small part of the anteromedial corner of the flange appears to be missing. The flange is greatly thickened dorsoventrally, but thins considerably toward its lateral apex. The ventral surface is convex and has a dense covering of teeth except for a narrow smooth margin along its posterior margin. The teeth

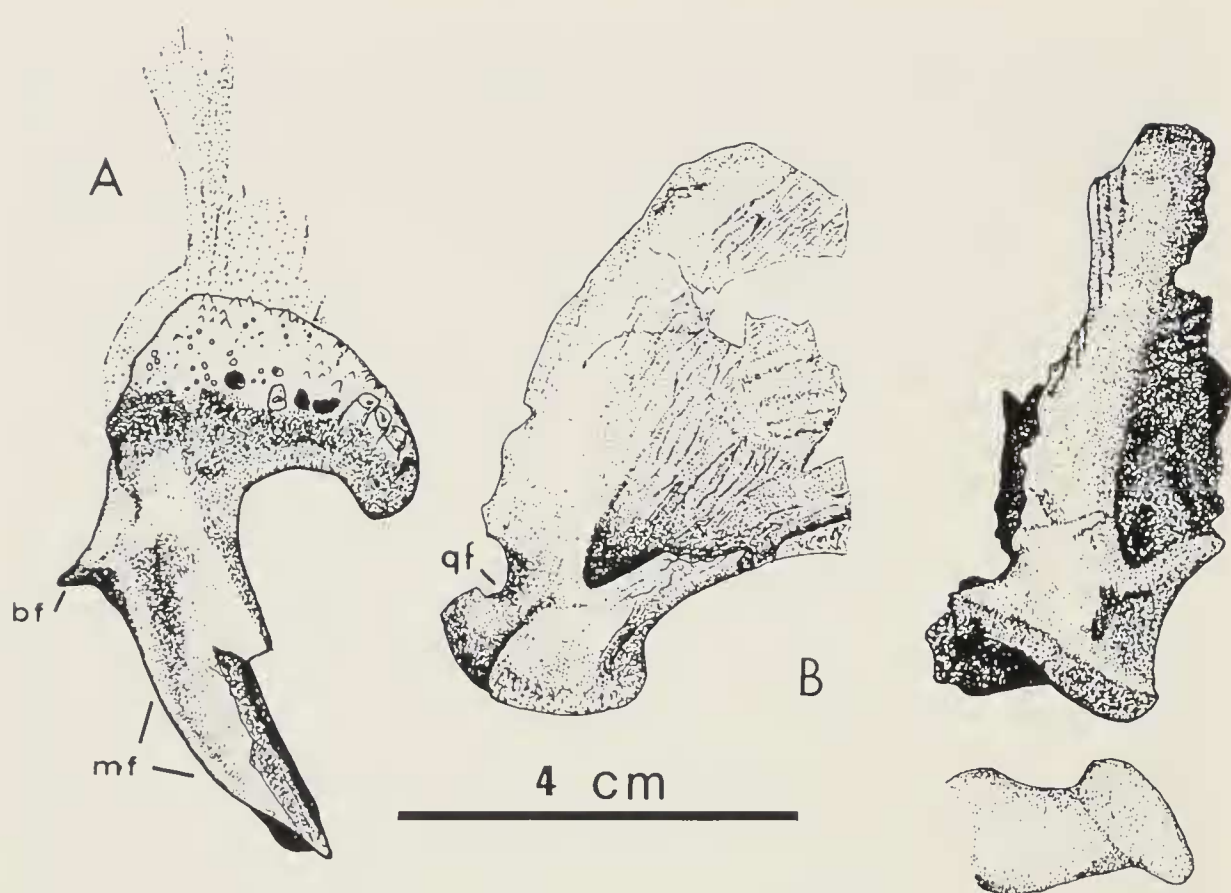


Fig. 3.—Palatal complex bones of *Limnoscelis dynatis*, holotype, CM 47653. A, ventral view of partial left pterygoid; B, medial, posterior, and condylar views of left quadrate. Abbreviations: bf, basiarticular flange; mf, medial flange; qf, quadrate foramen.

are blunt denticles, ranging in diameter from 0.3 to 0.8 mm, except for a single row of much larger teeth adjacent to the smooth posterior margin of the flange. Only the bases of the larger teeth are preserved, five of which can be discerned, but intervening spaces suggest a probable minimal count of eight. The tooth bases are about 2 mm in diameter and exhibit no obvious infolding.

Extending from the medial half of the posterior margin of the toothed, transverse flange is a massive triangular buttress that narrows posteriorly to form a thick, posterolaterally directed, keeled ventral edge of the quadrate ramus proper; the distal half of the ventral edge of the left pterygoid is broken away. Except for its ventral edge the quadrate ramus proper cannot be seen in the ventral view of the pterygoid in Fig. 3A. In transverse section it is a dorsomedially inclined lamellar structure, the dorsolateral surface of which contacted the dorsal lamella of the quadrate. A prominent, essentially horizontal flange, here referred to as the medial flange, projects medially from the quadrate ramus proper. Anteriorly, the ventral edge of the quadrate ramus proper projects about 8 mm below the level the ventral surface of the medial flange, but diminishes gradually in height almost completely posteriorly. The smooth rounded edge of the medial flange curves gradually posterolaterally as it terminates at the distal end of the quadrate ramus proper. A small, vertical flange extends both posteromedially from the medial surface of the quadrate ramus proper and dorsally from the anterior margin of the medial flange. The small vertical flange, here referred to as the basiarticular flange, extends a short distance medially beyond the medial flange. The basiarticular flange of



the left pterygoid appears to be nearly complete, and its posterolateral surface undoubtedly contributed greatly to the articular surface for the basipterygoid process of the braincase. The quadrate ramus proper, medial flange, and basia-articular flange merge to form the lateral and dorsal, ventral, and anterior walls, respectively, of a deep, subconical recess (not visible in Fig. 3A), the apex of which is directed anterolaterally. The recess must have been at least partially occupied by the articulated basipterygoid process.

*Quadrate.*—The quadrates are the only elements of the palatoquadrate cartilage preserved. The left one is nearly complete and exposed in medial view (Fig. 3B) and the less complete right one (not illustrated) in lateral view. The quadrate consists of two components: a broad, subtriangular dorsal lamella that articulates with the quadrate ramus of the pterygoid medially and the squamosal and quadratojugal posteriorly; and a ventral, stout condyle that articulates with the quadratojugal laterally. The sutural scar for the pterygoid is subtriangular, extending anteriorly from an acute angle near the base of the condyle. It closely follows the ventral margin of the dorsal lamella, and although the exact limit of its anterodorsally trending border is indistinct, it appears to parallel but be separated by a narrow margin from the posterodorsal margin of the dorsal lamella. At the posterior end of the ventral border of the pterygoid scar the quadrate forms a distinct medial shelf that supports the posterior portion of the ventral edge of the quadrate ramus of the pterygoid. The posterior margin of the dorsal lamina forms a very narrow, laterally projecting shelf. The striated surface of the shelf was overlapped by the squamosal along its wider dorsal half and probably by the quadratojugal along its narrower ventral half. There is a smooth, semicircular notch for the quadrate foramen in the posterior margin of the dorsal lamella just above the condyle. It is presumed that the deep excavation above the medial condyle adjacent to the posteroventral corner of the pterygoid suture is the stapedia recess that received the distal end of the quadrate process of the stapes. The depth of the recess is exaggerated by the ventral medial shelf of the lamina. The entire lateral surface of the dorsal lamina was free and has a smooth, slightly concave surface.

The articular condyle is transversely expanded and in ventral view is divided into a pair of oval condylar facets, with the narrower, shorter medial condyle being positioned somewhat anterior and ventral to the lateral condyle. The long axis of the lateral condyle trends anteroposteriorly, whereas that of the medial condyle is anterolaterally oriented.

### Braincase

*Basiparasphenoid.*—The braincase is preserved in three major components: the basiparasphenoid, otic-occipital, and sphenethmoid. The basiparasphenoid (Fig. 4A) is uncrushed and complete except for the absence of all but the base of the anterior rostrum or cultriform process, which is heart-shaped in transverse section, tapering to a sharp midline angle ventrally. Its smoothly rounded dorsolateral edges border a narrow, troughlike, midline groove that held the ventral edge of the sphenethmoid. At the posterior end of the groove is a small, prominent tubercle of unknown function. The basipterygoid processes are very stout and have a triangular outline in dorsal and ventral views, with the anterior margin being transverse. In anterior view, the flat anterior surface of the processes are also triangular in outline, with the lateral apex of the triangle formed by the ventrolaterally sloping margin of the dorsal surface and the horizontal margin of the

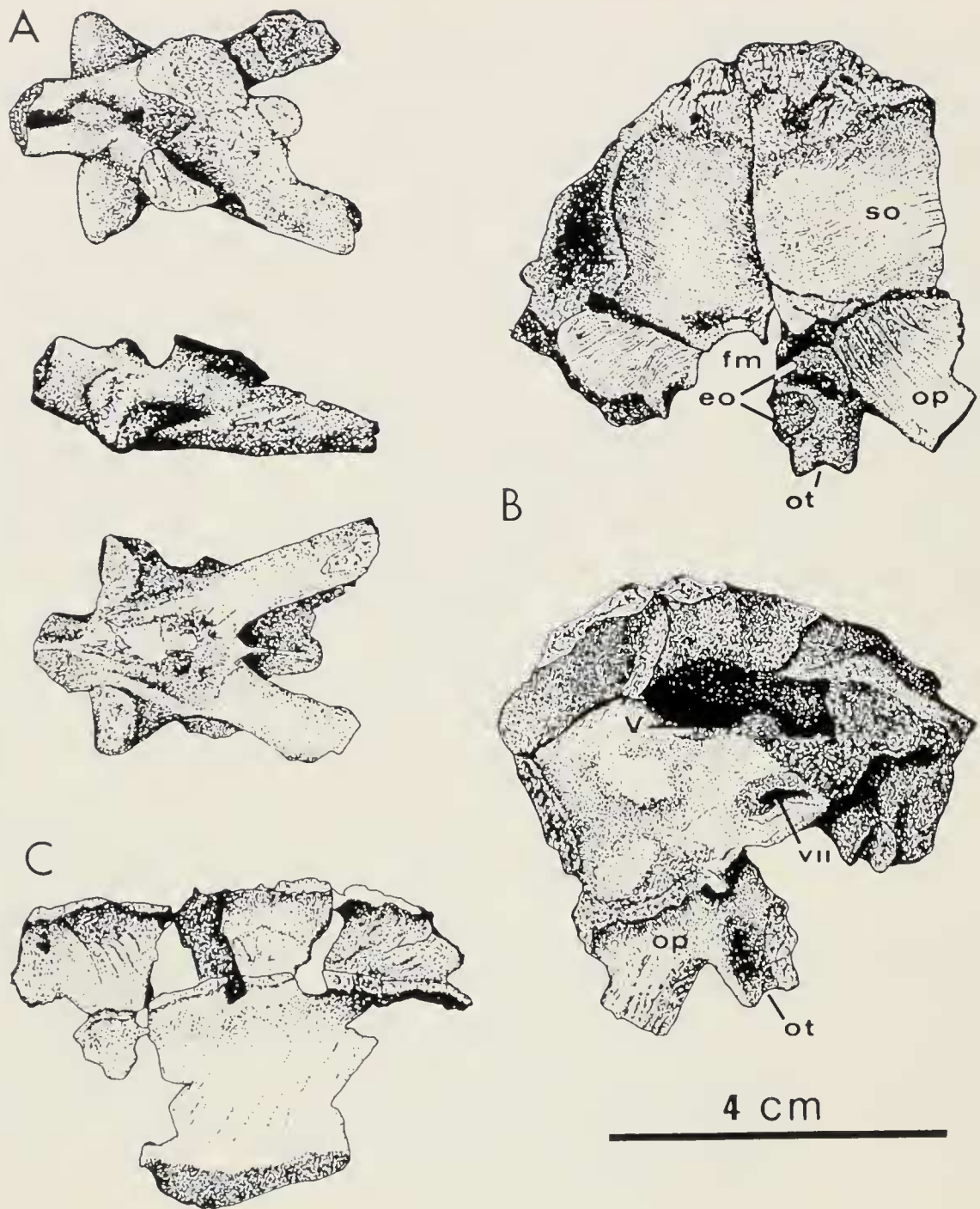


Fig. 4.—Braincase of *Limnoscelis dynatis*, holotype, CM 47653. A, dorsal, left lateral, and medial views of basiparasphenoid; B, occipital and right lateral views of otic-occipital complex; C, left lateral view of sphenethmoid. Abbreviations: eo, sutural scar for exoccipital; fm, foramen magnum; op, opisthotic; ot, otic trough; so, supraoccipital; V, VII, foramina for cranial nerves.

ventral surface of the process. The area of articulation of the process covers the entire slightly convex dorsal and anterior surfaces, then curves posteroventrally onto approximately the anterior two-thirds of the ventral surface.

Posterior to the rostrum and its small midventral tubercle is the deep, smoothly finished depression of the retractor pit for the origin of the retractor bulbi and bursalis muscles. A foramen on the midline of the anterior margin of the pit floor was probably for the exit of the internal carotid artery. A very small median ridge divides the pit floor immediately posterior to the foramen. The space above the



pit floor would have been occupied by the pituitary body as the sella turcica. The retractor pit is bounded laterally by smoothly rounded, posteriorly diverging ridges, the processus clinoides. Posteriorly, the processus clinoides rises dorsally into a moderately high projection, the processus sellaris, the flat, unfinished dorsal surface of which is roughly triangular in outline. Although the right processes sellaris is incomplete, the left appears to be complete. The processi sellares are ossifications of the ventral portions of the pila antotica and bound the dorsum sellae laterally. The latter is typically a transverse vertical sheet of bone that separates the sella turcica from the cranial cavity. A true dorsum sellae formed by the basisphenoid appears to be absent, as is also shown by Fracasso (1987) for *Limnoscelis paludis*.

Posterior to the basiptyergoid processes the basiparasphenoid expands laterally. In dorsal view the expansion appears as a triangular plate whose posteromedial border is strongly emarginated due mainly to loss of bone. The posterolateral winglike processes formed by the emargination are the distal ends of the cristae ventrolaterales, which are prominently defined in ventral view of the complex. The unfinished dorsal surface of the posteriorly expanding plate was obviously overlapped by the otic-occipital portion of the braincase. On the more complete left side of the triangular plate a very shallow troughlike depression that assumes the full width of the cristae ventrolateralis extends anteromedially along the lateral margin of the plate to the processus sellaris. This groove almost certainly marks the course of the anterior prootic portion of the otic-occipital portion of the braincase. It is therefore likely that the prootic not only contacted the dorsal surface of the processus sellaris, but may have also formed the greater portion or all of the dorsum sellae.

On the ventral surface of the basiparasphenoid a narrow, slightly raised mid-ventral area extends between the levels of the anterior and posterior borders of the basiptyergoid processes. Though much of the central portion of the raised area is broken away, its slightly rugose surface does not appear to have supported teeth or denticles. Several minute parallel grooves and ridges run along the base of the basiptyergoid processes. Posterior to the processes the entire lateral borders of the posterior triangular portion of the complex are dominated by the thick, vertically raised, sharply demarcated rounded ridges of the cristae ventrolaterales. The cristae merge anteromedially to form a deep, concave posteromedial border. The posteroventral edge of the internal margin of the apex of their union extends in liplike fashion a few millimeters posteriorly. A thin, posteriorly incomplete, central sheet of bone spans the dorsomedial edges of the cristae ventrolaterales at the apex of their internal union. The sheet is divided along its midline by a thin ridge that expands slightly as it joins the posterior surface of the joined cristae and forms the median boundary between a pair of anteriorly directed, shallow pockets.

*Otic-occipital.*—The otic-occipital component (Fig. 4B) is represented by both fused prootic-opisthotic complexes and the supraoccipital; the exoccipitals and basioccipital are absent. The right side of the preserved otic-occipital component is considerably more complete than the left, though a significant portion of its anterior (prootic) end of the right otic capsule is also absent. The complex has been significantly distorted. A major break extending dorsally from the foramen magnum roughly divides the occiput. The right half of the occiput, displaced a half centimeter dorsally relative to the left half, has been rotated a few degrees counterclockwise so that dorsally it overlaps by at most about a half centimeter

the occipital surface of the left half. The right opisthotic has been displaced medially about 7 mm along its suture with the supraoccipital. The right otic capsule (except the opisthotic portion that contributes to the occiput) has been crushed medially relative to the occiput, exaggerating its anteromedial orientation so that its lateral surface now faces almost directly anteriorly. This distortion is expressed by a major break extending posteriorly from the right fenestra ovalis to the occiput.

The essentially complete supraoccipital dominates the occiput, and its surface sculpturing consists of fine, parallel striation that extend laterally from the midline. Its sutural contact with the opisthotic extends directly dorsolaterally from near the dorsolateral edge of the foramen magnum to the edge of the exposed surface of the occiput. At this point it is assumed that the contact turns abruptly dorsally across the depressed, posterolaterally facing, unfinished sutural surface for the tabular that is composed by the supraoccipital and the prootic portion of the otic capsule. Close to the dorsal margin of the jointly formed sutural surface, the contact turns strongly medially as it continues across the smoothly finished dorsal surface of the lateral wall of the dorsally open braincase. The exposed occipital surface of each half of the supraoccipital is broadly concave in horizontal section. A large roughened area along the dorsal margin of the supraoccipital that expands ventromedially in a low convex arc marks the overlapping contact of the postparietal. The nearly vertical lateral margins of the supraoccipital contacted the medial expansion of the tabular, termed the tabular cone in *Limnoscelis paludis* by Fracasso (1987). The supraoccipital forms a smooth archlike dorsal margin of the foramen magnum.

The opisthotic portion of the occiput forms most of the lateral surface of the internal wall of the foramen magnum, as the exoccipital articulates with the posterior surface of the opisthotic adjacent to the lateral margin of the foramen. Judging from the more complete and undistorted left side of the foramen, the opening appears to have been vertically oval with the dorsal end narrower. In occipital view, the opisthotic expands laterally into a prominent paroccipital process, and ventrally and slightly laterally into a process that Fracasso (1987) termed the otic trough in *Limnoscelis paludis*. Though incomplete distally, the right paraoccipital is far more complete than the left. From its greatly thickened region near the foramen magnum the paroccipital process thins to only about 2 mm at its incomplete free, distal margin. The occipital surface of the process is slightly concave, curving posteroventrolaterally distally, and exhibits a sculpturing pattern of fine, parallel striations that extend from its contact with the supraoccipital to its distal margin. The anterior surface of the paroccipital process is flat and exhibits a cancelous surface. The otic trough is narrowly rectangular, with the distal margin being slightly concave, and is separated from the paroccipital process by a deep, sharply angular notch with smoothly rounded margins. Paired facets for the exoccipital are present on the lateral margin of the foramen magnum on both opisthotics, but only the more complete right pair of facets are fully visible in occipital view. At the dorsomedial corner of the opisthotic is a slightly convex, kidney-shaped, roughened articular facet surrounded by a low, smooth ridge. The second facet for the exoccipital is separated from the ventral margin of the first by a narrow, slightly depressed strip of smoothly finished bone. It is semicircular with a smooth, low ridge surrounding its flat, roughened surface. The narrow strip of smooth bone separating the pair of facets undoubtedly marks the internal passage of the jugular foramen, which typically exits at the exoccipital-opisthotic union and presumably transmitted cranial nerves IX-XI and the jugular vein. At



the lateral end of the narrow strip of smooth bone a small foramen of unknown function penetrates the opisthotic.

The otic trough in *Limnoscelis paludis* is described by Fracasso (1987) as a troughlike projection that borders the fenestra ovalis posteromedially. Nearly the entire distal length of the anterolaterally facing surface of the otic trough in *L. dynatis* is excavated into a deep basin of finished bone with some irregular ridges. The thin lateral edge of the trough was undoubtedly free. All but a short, free distalmost portion of the medial edge of the trough is greatly thickened and probably contacted the basioccipital-exoccipital complex medially. The proximal end of the trough terminates in a thick, smoothly rounded ridge that is the posterior lip of the fenestra ovalis proper. The remaining portion of the right lateral surface of the braincase above the level of the fenestra ovalis is interpreted as the prootic region of the otic capsule. The smoothly finished lateral surface of the prootic region is broadly convex in transverse section and narrows considerably in vertical width anteriorly. The crest-like dorsal portion of the supraoccipital that is overlapped posteriorly by the postparietals projects above the posterior border of the dorsally opened brain cavity. The posterior and lateral walls of the brain cavity are formed by the supraoccipital and the fused prootic-opisthotic complexes, respectively, and their rims are smoothly finished and sculptured with short, prominent irregular ridges. Two oval swellings on the posterior lateral surface of the prootic region probably indicate the positions of semicircular canals of the inner ear. Near the anterior end of the dorsal margin of the preserved right prootic region is a smooth, broadly concave notch for the exit of the trigeminal nerve (V). The Vidian foramen for the palatine branch of both the facial nerve (VII) and the internal carotid is located near the ventral margin of the anterior end of the preserved right prootic region. The anterior margin of the foramen has an anteriorly narrowing groove-like extension. There is no synotic bone, nor sutural evidence of its former presence. Fracasso (1987:11) described the synotic in *Limnoscelis paludis* as “a small median wedge-shaped element situated posterodorsally between the otic capsules . . . tightly apposed against the overlying anteroventral surface of the supraoccipital.”

*Sphenethmoid.*—The greater part of the sphenethmoid is preserved (Fig. 4C), lacking mainly the anterior and posterior margins. In transverse section it is Y-shaped and consists of two components: a thin ventral interorbital septum and a dorsal V-shaped trough formed by dorsolateral, winglike flanges between which the anterior end of the brain and its olfactory tract were channeled. The sphenethmoid has been severely crushed laterally so that the dorsolateral wings of the dorsal component are narrowly separated along the midline. The crushing is revealed in lateral view by a longitudinal break in the dorsolateral wing that occurs just above and along the full length of the union of the wing and the interorbital septum. Except for a very narrow margin along the ventral edge of the interorbital septum, the lateral surfaces of both components of the sphenethmoid are smoothly finished and ornamented by fine, irregular vertical ridges. Those of the interorbital septum become more pronounced near its ventral border.

The ventral margin of the interorbital septum is thickened into an unfinished, keellike structure. The keel is roughly diamond-shaped in transverse section, and its medially merging, ventrolateral margins undoubtedly inserted into a middorsal groove in the cultriform process of the parasphenoid. On contacting the ventral surface of the skull roof the dorsolaterally wings of the dorsal component are extended laterally as a gradually thinning margin, producing a rather wide, dorsally

facing rugose sutural surface. In lateral view, the dorsolateral wings decrease slightly in height posteriorly and appear to curve slightly ventrally. The ventral portions of the posterior margin of both wings are complete enough to note that they terminate in a concave arcuate border a few millimeters short of the posterior end of the dorsal margin of the interorbital septum. The posteriorly protruding portion of the interorbital septum is transversely thickened into an equilateral triangle with dorsomedially converging sides. Its posterior surface is concave and unfinished and may have been continued posteroventrally as the cartilaginous pila antotica, which joins the processi sellares of the basiparasphenoid complex with the sphenethoid.

### Lower Jaw

*Dentary.*—Portions of both dentaries are preserved (Fig. 5A, 11B). The right is represented by the anterior symphyseal region and includes the first, second, fourth, and fifth teeth, with only the tip of the crown of the fifth being lost. Tooth positions 3 and 6 are represented by sockets. The anterior lateral surface of the dentary at the level of tooth positions 2 and 3 exhibits a pronounced swelling. The anterior medial surface forms a flattened, rugose symphyseal area that extends posteroventrally from the base of the first tooth. Posterodorsal to the symphyseal surface is a smoothly finished, subtriangular area that extends between the bases of teeth 1 and 5, and was undoubtedly exposed on the medial surface of the articulated jaw. Long, posteroventrally directed striae run along the ventral margin of the medial surface of both dentaries that begin immediately behind the symphyseal surface and mark the contact with the splenial. Only about the anterior half of the lateral surface (posterior half covered by the right shoulder girdle) and the entire medial surface of the left dentary is exposed. It is nearly complete except for lacking much of the symphyseal region and a narrow margin along its posterior border. Approximately the first three teeth of the symphyseal region are lost except for what appears to be a replacement tooth of the first. Above the sutural surface for the splenial the smooth, slightly concave surface of the Meckelian canal narrows anteriorly, ending at about the level of the fourth tooth position. The canal is bordered dorsally by a thick, posteriorly narrowing dental shelf that is rectangular in transverse section. Horizontal striae along its medial surface clearly indicate the contacts of the coronoid and prearticular. It appears that the labial side of the dental shelf overlaps the bases of the teeth only very slightly more than that of the lingual side.

It is estimated that the dentary held as many as 23 or 24 teeth. The first two teeth are identical in shape and considerably larger than those of the rest of the series. The second is the largest, measuring 30 mm in length and 11 mm in greatest basal diameter, whereas the same measurements for the first tooth are 23 and 10 mm, respectively. Their basal halves are anteroposteriorly oval in cross-section and constant in width. The distal halves taper to a point and are modestly curved posteriorly and slightly medially. The third tooth is not represented. The fourth tooth of the right dentary is 12 mm in length, and its anteroposteriorly oval base is 6 mm in greatest diameter. The teeth between the fourth tooth and the end of the series decrease gradually in size. The crowns of teeth four to thirteen taper to a point and are curved posteriorly, but become progressively less so posteriorly. These teeth exhibit a sharp, very narrow, low ridge that extends along the full anteromedial and posterolateral lengths of the crown, passing through the crown



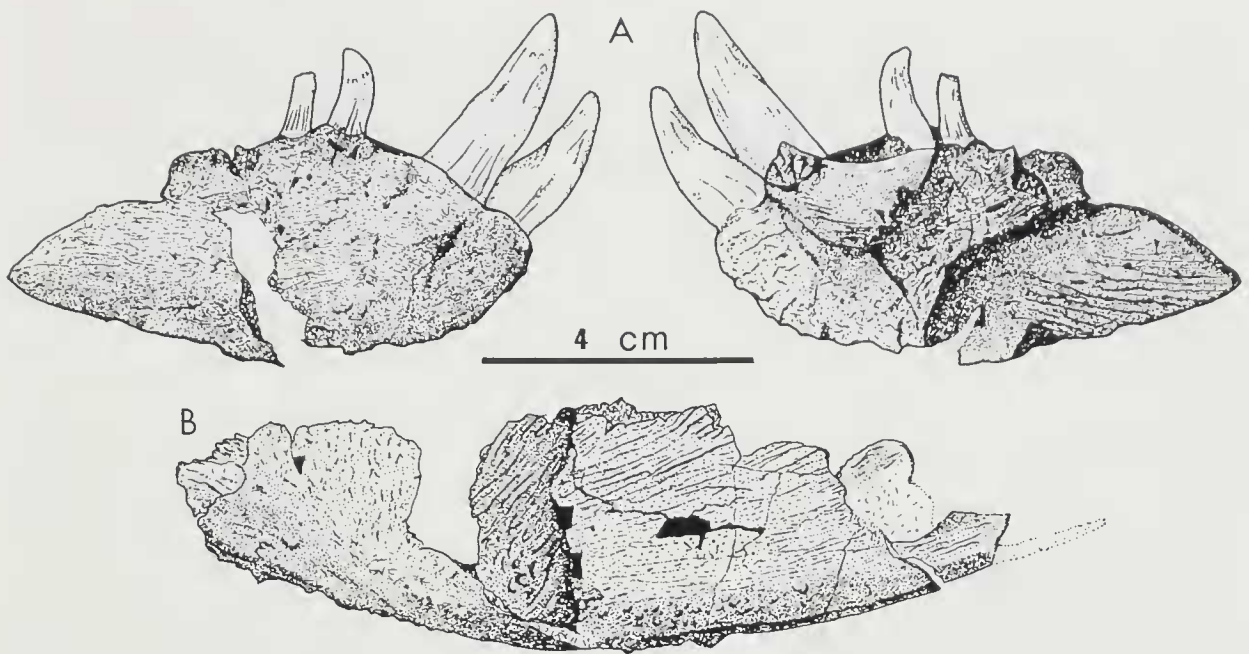


Fig. 5.—Lower jaw bones of *Limnoscelis dynatis*, holotype, CM 47653. A, lateral and medial views of anterior portion of right dentary; B, lateral view of incomplete probable right angular.

tip. The ridge becomes progressively less distinct on more posterior teeth. The crowns of the last teeth of the series appear to be blunt.

Three tooth-bearing fragments, probably of a single left dentary, are included in the paratype CM 47651 (formerly UCLA VP 1737). One of the fragments was briefly described by Vaughn (1972). A small portion of a large dentary of the paratype CM 47652 (formerly UCLA VP 1699) was mistakenly described by Vaughn (1969) as a right palatine.

*Angular.*—The only other element of the lower jaw represented is a right angular (Fig. 5B). It is exposed only in lateral view, and, although the external portion is nearly complete, most of its dorsal sutural margin is lost. The angular preserves the ventral convex margin of the posterior half of the mandible.

### *Postcranial Skeleton*

#### **Axial Skeleton**

Williston's (1911a, 1912) general description of the vertebral column of *Limnoscelis paludis* reported minimal change along the presacral column. He described conspicuously swollen neural arches, homogeneous proportions of the neural spines, and little change in the sizes of the centra. Only about 40% of the presacral column of the holotype of *L. dynatis* is preserved, but as disarticulated and mainly incomplete elements. Yet, the presacral column exhibits considerable variability, as is undoubtedly true of *L. paludis*.

*Vertebrae.*—Of the 26 vertebrae of the holotype, those assigned to regional positions include two cervicals, eight dorsals, and 13 caudals. No elements of the atlas-axis complex or the sacrum are present, and the only intercentral element represented is a haemal arch. None of the vertebrae possess any secondary articulations such as hyposphenes or episphenes, nor do any exhibit a neurocentral suture. The centra are amphicoelous and notochordal.

Of the two vertebrae identified as cervicals, the one illustrated in Fig. 6 is 33% wider, though its centrum is only 5% or 6% wider and longer. The cervical vertebrae are squat, and the centra are spool-shaped, with the horizontal diameter of the ends exceeding the length by only about 12%. The ends of the centra flare outward strongly to form an expanded subcircular liplike rim that surrounds the notochordal funnel. As a result the lateral margins of the centrum appear deeply concave. In all of the vertebrae there is on the dorsal margin of the anterior rim of the centrum a pair of small protuberances that mark the anteriormost points at which the neural arch pedicles join the centrum. There is little beveling of the ends of the centra to accommodate the intercentra. The midventral margin of the centrum forms a narrow, flattened surface or a very shallow, troughlike depression that in lateral view appears slightly concave and to reach nearly the ventral margins of the centrum rims. The transverse processes of the cervical vertebrae are strongly developed and project directly laterally well beyond the zygapophyses. In lateral view the upper or diapophyseal portion of the process, which extends from the neural arch pedicle, is thick and roughly circular in cross-section. The ventral or parapophyseal portion extends diagonally anteroventrally across the centrum as a thin web of bone to a point about midheight along the anterior rim of the centrum. In anterior or posterior view the process is winglike and becomes steadily reduced in lateral extent anteroventrally until it pinches out or is reduced to a very low ridge on the centrum rim.

The neural arches of all the presacral vertebrae are swollen, with the zygapophyses extending laterally well beyond the lateral margins of the centra. The cervical neural arches are less swollen and the pedicles proportionally longer than those of the dorsal vertebrae. The anterior zygapophyses are directed anterolaterally, with the articular plane tilting ventromedially and posteroventrally at about 30° and 25° from the horizontal, respectively. The articular planes of the posterolaterally directed posterior zygapophyses appear to be far less angulated. On the midline of the anterior and posterior surfaces of the neural arch is a triangular fossa for attachment of the interneural tendons. A thin shelf of bone separates the fossae from the ventral neural canal. The anterior fossa is continued dorsally along the anterior edge of the neural spine as a deep rectangular groove. The spines of the cervical vertebrae are low, transversely narrow, and moderately elongate anteroposteriorly. The cervical neural arch exhibits furrows immediately lateral to and parallel with the neural spine. A pronounced shallow fossa is present on the anterior surface of the posterior zygapophyses.

The dorsal vertebrae (Fig. 7) differ from the cervicals mainly in proportions, size, and structure of the transverse processes and neural spines. The centra of the dorsals are very short and have a disclike appearance, with the diameters of the subcircular ends exceeding the lengths by as much as 60 to 80%. The centrum rims are far more strongly flared laterally than in the cervicals, and in end or lateral view appear to have pronounced secondary liplike structures on their ventral margins. In lateral view these flanges slope back slightly from the centrum rims apparently to accommodate the intercentrum. The secondary liplike structure of the posterior rim is considerably more developed than that of the anterior rim, including almost the ventral half of the rim and projecting farther ventrally. The ends of the notochordal canal are not truly funnel-shaped, as the tip of the constricted end expands into a dome-shaped cavity. Paired, longitudinal ridges delimit a deep, narrow midventral depression on the centrum. In lateral view, they curve ventrally to join the liplike flanges of the centrum rims.



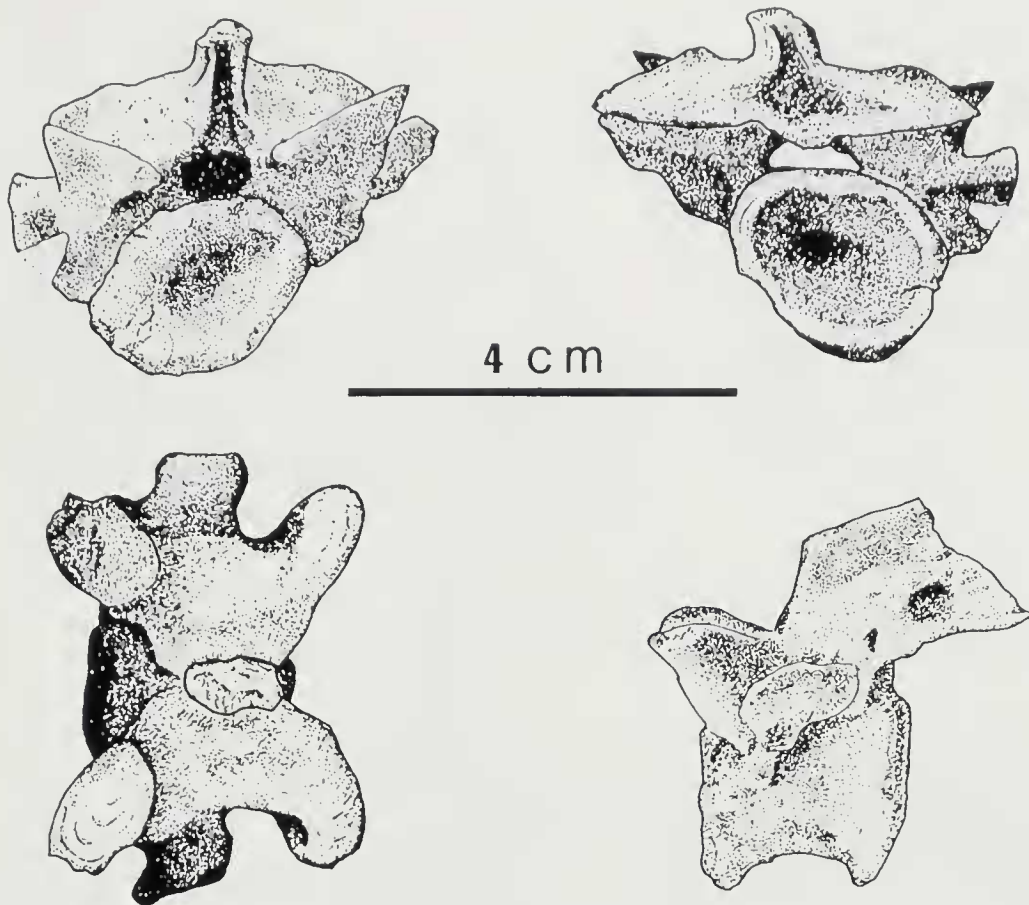


Fig. 6.—*Limnoscelis dynatis*, holotype, CM 47653. Anterior, posterior, dorsal, and left lateral views of cervical vertebra.

The transverse process in what are probably middorsal vertebrae (Fig. 7A) is a laterally projecting, thin, winglike structure. In lateral view, the process extends diagonally anteroventrally in a broadly sigmoidal curve from the posterior surface of the anterior zygapophysis to a point about midheight along the anterior rim of the centrum. The rib facet expands at both ends to form well-defined tubercular and capitular areas. In end view of the vertebrae the process diminishes in lateral extent as it extends anteroventrally, so that the facets face ventrolaterally, with the tubercular facet being positioned farther laterally than the capitular facet. In what is probably a posterior dorsal vertebra (Fig. 7B) the transverse process is merely a short, pronounced ridge that extends diagonally anteroventrally across the base of the anterior zygapophysis to the centrum rim. The facet shows no constriction into tubercular and capitular areas. In another dorsal vertebra (Fig. 7C) the transverse process is a narrow, low ridge that extends nearly vertically from the base of the anterior zygapophysis to a point midheight along the centrum rim. It appears to lack an articular facet for the rib, and the vertebra is probably from the posterior end of the dorsal series.

In comparison to the cervical vertebrae, the tilting of the zygapophyseal planes of the dorsal vertebrae is about the same ventromedially but considerably less posteroventrally. As in the cervical vertebrae, there is a distinct fossa on the anterior surface of the posterior zygapophysis. The neural spines of the dorsal vertebrae have two fundamentally different morphologies. All but one of the preserved dorsals possess tall, columnar neural spines that become progressively

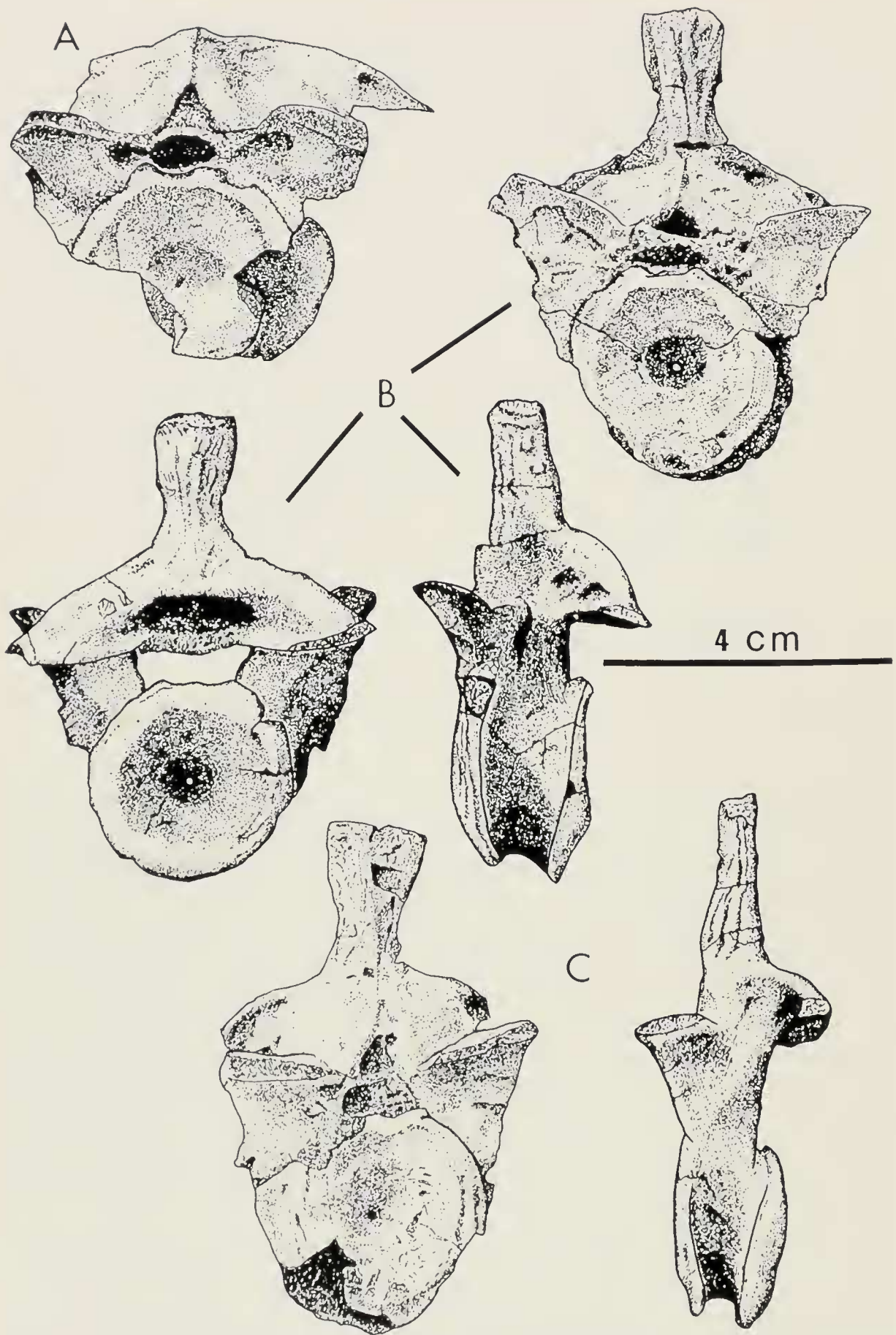


Fig. 7.—Dorsal vertebrae of *Limnoscelis dynatis*, holotype, CM 47653. A, anterior view of probable middorsal; B, anterior, left lateral, and posterior views of posterior dorsal; C, anterior and left lateral views of far posterior dorsal.



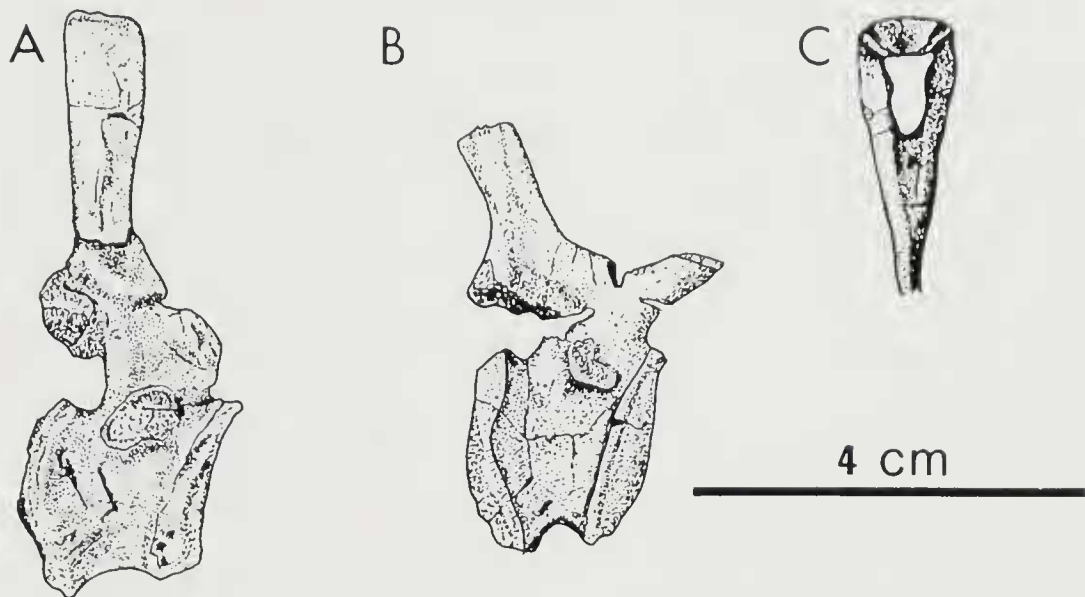


Fig. 8.—Caudal vertebrae of *Limnoscelis dynatis*, holotype, CM 47653. Right lateral views of A, far anterior, and B, anterior caudals; C, haemal arch in anterior view.

more oval as they increase in transverse width toward the dorsal tip. A sharp, narrow, low ridge runs the entire midline length of the anterior and posterior surfaces of the spine. Much smaller irregular ridges frequently lie close to and subparallel with the main midline ridges. In at least one dorsal, believed to be a middorsal (Fig. 7A), the neural spine consists only of a very low, narrow ridge. Despite the disarticulated nature of the holotype, the extreme differences in neural spine construction would not appear to indicate regional variability in the vertebral column. Rather, we conclude that there was alternation in neural spine height and structure in at least part of the presacral column. This phenomenon is quite common in a wide variety of late Paleozoic tetrapods and occurs in the holotype of *Limnoscelis paludis* (Sumida, 1990).

Vertebrae are the most likely skeletal elements of *Limnoscelis* and *Desmatodon* to be confused, which like all diadectomorphs are very similarly constructed. Features that distinguish postcervical dorsals of *Limnoscelis* from those of *Desmatodon* include: 1) absence of episphenes and hyposphenes; 2) much shorter columnar neural spines; 3) diameter of the centrum is greater relative to the width of the expanded neural arch, and in end view the vertebrae (not considering the neural spine) appear much more expanded; and 4) the apex of the funnel-shaped ends of the notochordal canal have a dome-shaped expansion.

Several of the preserved caudal vertebrae are nearly complete, two of which may be from near the anterior end of the series (Fig. 8A, B). The centra have vertically elongated diameters, and their height-to-width ratios measured across the anterior end of the centrum are about 1.5. The relatively high vertical diameter may be due in part to depositional compression. In a larger more anterior caudal (not figured), the centrum rims are nearly circular, particularly the posterior rim, which has transverse and vertical diameters of about 21.5 and 20.5 mm, respectively. As in the dorsal vertebrae, the ventral portion of the centrum rims are expanded by the presence of a secondary liplike structure, and that of the posterior rim is more developed and projects farther ventrally. In the two figured caudals, the centrum has a deep, narrow, midventral channel that posteriorly divides the ventral lip of the centrum rim into two short, stout protuberances that provide

posteroventrally facing facets for articulation with the haemal arch. In lateral view, the protuberances project anteroventrally to give the centrum a strongly beveled appearance.

In all of the caudals the transverse processes are positioned on the upper level of the centrum near the anterior centrum rim and are short, projecting only a few millimeters from the centrum. The process of the anteriormost preserved caudal is the largest of the series, projects laterally only a few millimeters, and its base extends posteroventrally to within a short distance of the posterior rim at about midheight of the centrum. The facet faces laterally and slightly posteroventrally, and its narrowly oval outline coincides with that of the cross-section of the process. The processes of the more posterior anterior caudals are reduced to low protuberances high up on the centrum, with much smaller, circular to oval, laterally facing facets. The neural arch of the anteriormost preserved caudal (not figured) is slightly expanded or swollen, whereas those of the more posterior anterior caudals are not noticeably expanded. The zygapophyses do not extend far beyond the lateral surfaces of the centrum, and their articular planes are steeply inclined. Except for some minor differences the neural spines of at least the anterior caudals are tall, bladelike, and inclined posteriorly. The neural spine of the anteriormost caudal (not figured) thickens laterally near its tip so as to be subcircular in cross-section but remains constant in anteroposterior width. It exhibits irregular vertical ridging on its lateral surfaces. The neural spines of the more posterior two anterior caudals (Fig. 8) are bladelike throughout their length, expand somewhat anteroposteriorly distally, and have relatively smooth lateral surfaces. There is no evidence of alternation in neural spine height and structure in the caudal series.

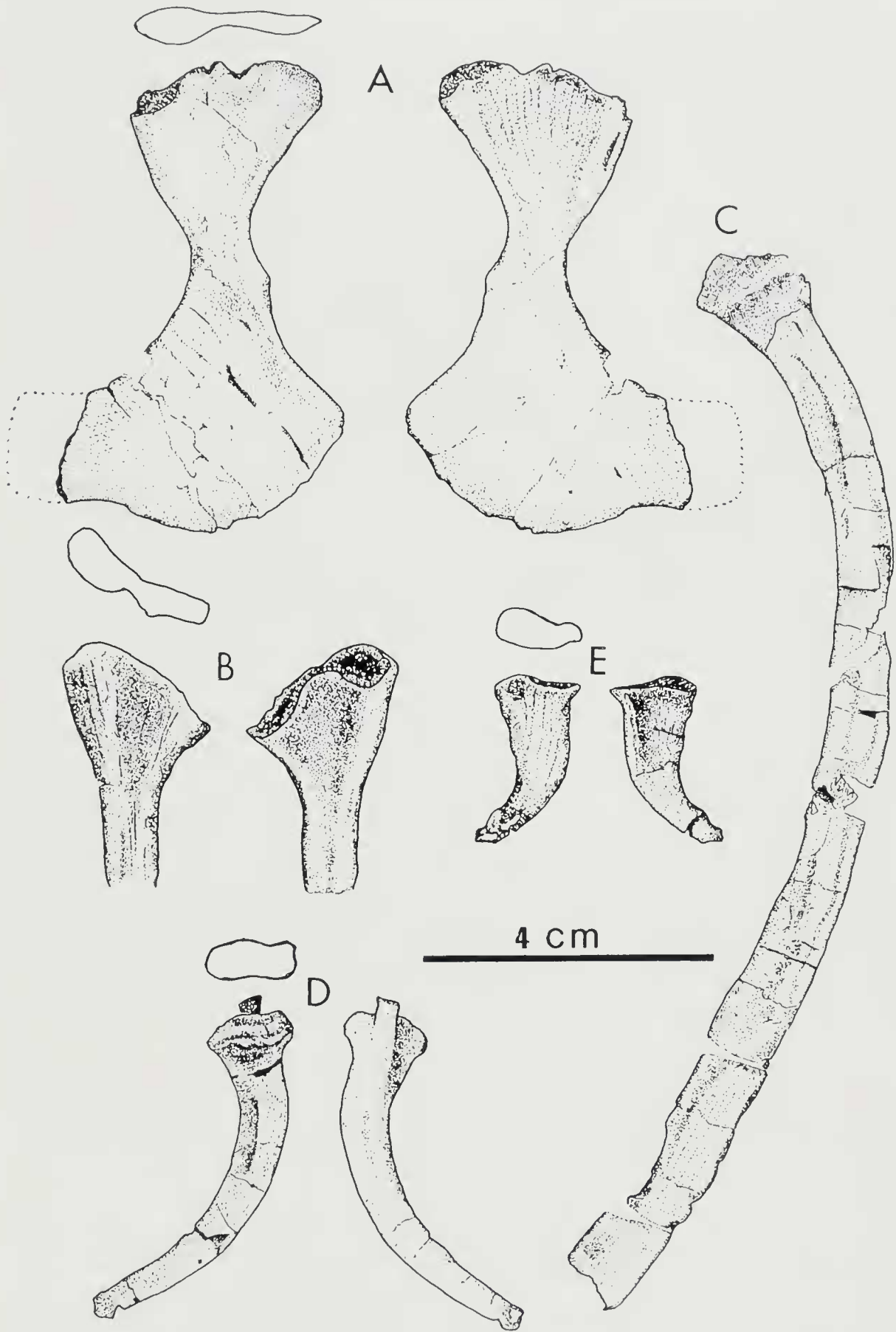
A single haemal arch, missing only the distal tip of the spine and preserved in anterior view (Fig. 8C), is assigned to the holotype. It has the typical Y-shaped chevron structure with the proximal crescentic intercentral crosspiece connecting the two arms of the Y. The roughened articular surface occupies the anterodorsal surface of the crosspiece. The enclosed space is slightly constricted laterally into the outline of an arrow head. The spine expands slightly anteroposteriorly distally so as to be bladelike.

*Ribs.*—Though numerous ribs are represented, few are complete enough to warrant description or illustration. Of the four complete or nearly complete cervicals, all are believed to be from the posterior end of the series, judging from Williston's (1912) description of *Limnoscelis paludis*. The greatly expanded proximal and distal ends occupy a single plane. Because the axis of the costal articular facet is oriented anteroventrally, the broad flat surfaces of the cervical rib (Fig. 9A) face anterodorsally and posteroventrally, with the leading and trailing edges being anteroventral and posterodorsal, respectively. The broadly expanded, flattened, triangular head occupies about one third of the rib length. Although the rib facet is single, it is clearly constricted into narrowly oval capitular and tuber-

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Fig. 9.—Ribs of *Limnoscelis dynatis*, holotype, CM 47653. A, anterodorsal and posteroventral views of cervical rib with outline of articular surface; B, anterodorsal and posteroventral views of right dorsal rib head with outline of articular surface; C, anterodorsal view of left dorsal rib shaft; D, dorsal and ventral views of far anterior caudal rib with outline of articular surface; E, dorsal and ventral views of posterior caudal rib with outline of articular surface.





cular areas of nearly equal length, but with the latter being substantially wider. The tubercular and capitular facets are partly visible in anterodorsal and posteroventral views of the rib, respectively. The anteroventral and posterodorsal edges of the rib head are thickened and rounded, producing a depressed triangular area between them on both the anterodorsal and posteroventral surfaces. The expanded proximal and distal ends of the rib are joined by a very short, narrow constriction of the shaft that is narrowly oval in cross-section. The expanded distal end is extremely thin and subtriangular in outline. In the figured rib (Fig. 9) only the somewhat elongated angle at the distal end of its posterodorsal margin is missing, and its outline has been restored on the basis of one of the other preserved cervical ribs. There is a low, triangular protuberance on the anteroventral margin of the shaft just distal to its narrowest point. The lateral margin of the distally expanded end of the shaft is broadly convex.

Numerous dorsal ribs are preserved, but none are complete. One rib head (Fig. 9B) is typical of the dorsal region of the column. The single articular facet is divided into a long, narrow, subrectangular capitular area and a shorter, wider, suboval tubercular area. Whereas the anterodorsal surface of the head is slightly convex except for a small, very shallow central depression, the posteroventral surface is almost completely occupied by a moderately deep basin. Also figured (Fig. 9C) is a presumed left dorsal rib missing the head; the shaft appears to be complete. In cross-section the shape and size of the shaft remains essentially constant throughout its length. A ridge extends along the anterodorsal surface of the proximal portion of the shaft. Two ribs identified as caudals are figured (Fig. 9D, E). Judging their marked difference in size, they are probably from near the beginning and the end of the first 11 or 12 members of the series. Williston (1912) described ribs of gradually decreasing size associated with only this region of the tail in *Limnoscelis paludis*. The outline of the articular facets of both ribs is similar. They are anteroposteriorly elongate and oval, widening considerably posteriorly, and have a shallow, concave constriction near the anterior margin of the ventral surface. The facets of both ribs are equal in length, but that of the more posterior rib is narrower. On the anterior margin of the ventral surface of the head is a short, ventrally directed ridge that extends medially to the facet margin. The ridge, which becomes higher medially, creates a shallow depression on the ventral surface of the rib head. The shafts are horizontally oval in cross-section and curve strongly posteriorly as they taper to a point. There is a thin, low ridge along the dorsal surface of the proximal portion of the shaft of the more anterior caudal rib. At the distal ends of the shafts of both ribs are very small, rounded protuberances.

#### *Appendicular Skeleton*

The preserved elements of the appendicular skeleton were found disarticulated. Missing elements include the cleithrum, interclavicle, carpus, and tarsus. Phalangeal bones associated with the holotype cannot be attributed positively to *Limnoscelis*.

*Clavicle*.—Only the right clavicle of the holotype is preserved (Fig. 10). It consists of a dorsal stem and ventral plate, and is essentially complete except for the tip of the dorsal stem and the posteromedial corner of the ventral plate. The two components meet in a smoothly curving, internal angle of about 110°. The ventral plate is slightly bowed ventrally, and its anterior margin is turned sharply upward to form a high ridge that diminishes as it extends dorsally onto the stem. In ventral view, the ventral plate is narrowly triangular and lightly sculptured by



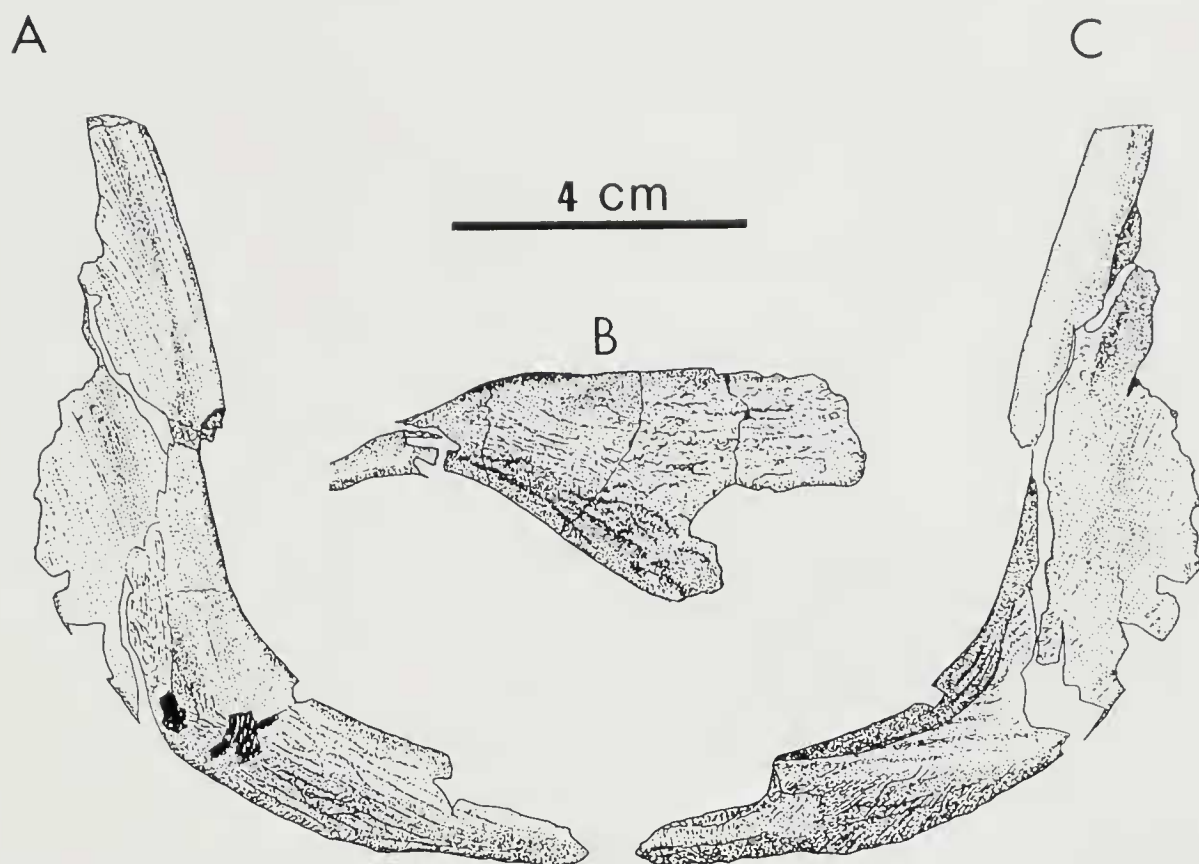
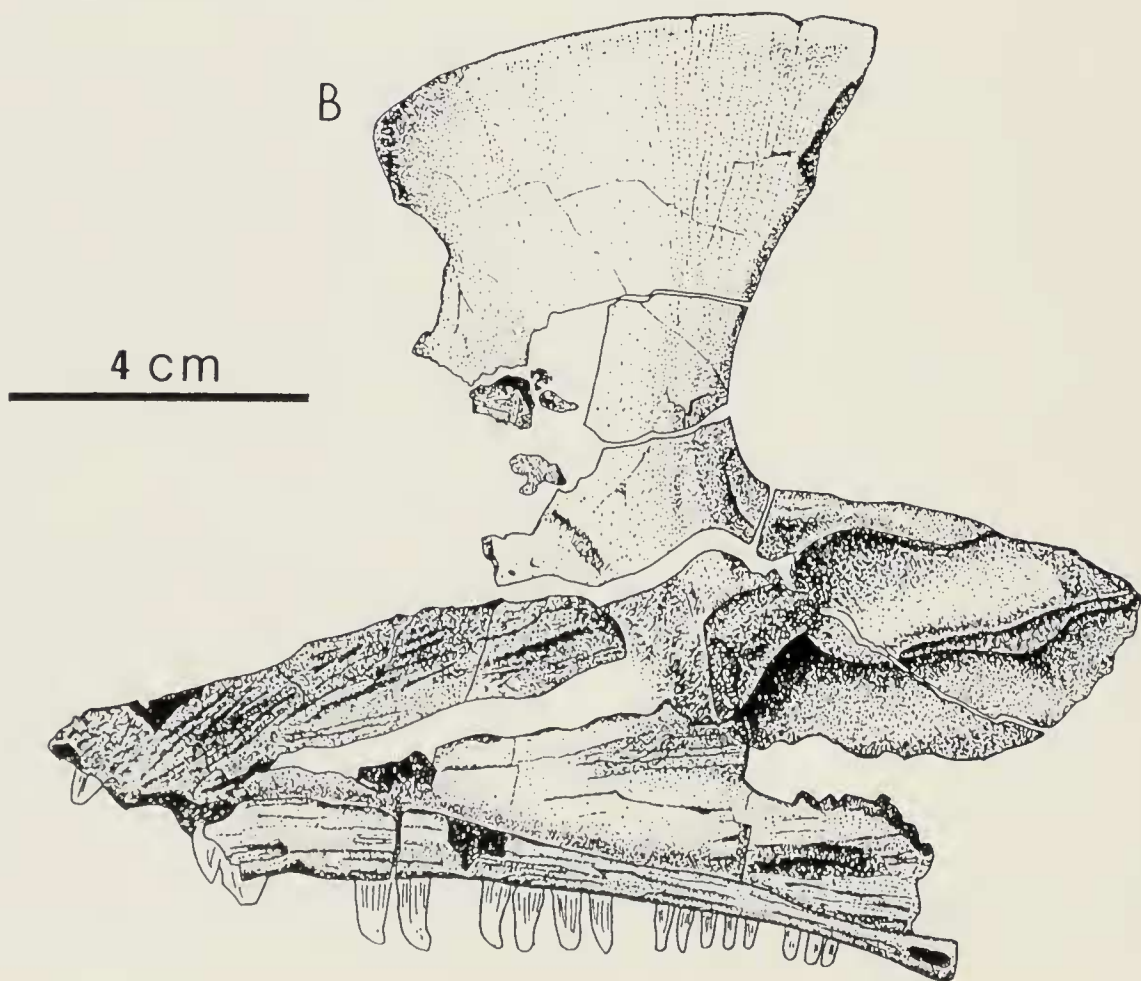


Fig. 10.—*Limnoscelis dynatis*, holotype, CM 47653. Anterior, ventral, and posterior views of right clavicle.

dense, transversely oriented striae. A deep immargination of the medial margin divides the ventral plate into subequal anterior and posterior blades. All but a small dorsal portion of the lateral margin of the stem is expanded into a thin, broad flange or lamina that projects laterally and slightly posteriorly to overlap most of the anterior margin of the scapulocoracoid. In posterior view, a narrow vertical groove along the dorsal portion of the union between the lateral flange and the dorsal stem proper may have received the ventral end of the cleithrum.

*Scapulocoracoid.*—Both scapulocoracoids (Fig. 11) are nearly complete and exposed in lateral view; the anterior coracoid region of the left element, however, is covered laterally by the left dentary but exposed (not figured) medially. There is no distinct suture between the scapular blade and the coracoid plate. The scapular blade is short but broad anteroposteriorly, and its slightly convex dorsal margin is thin and smoothly finished. Whereas the anterior border is vertically straight, the posterior border curves slightly posteriorly as the blade expands distally. Williston (1911a) and Romer (1946) both assumed the presence of an extensive cartilagenous suprascapula in *Limnoscelis paludis*. If a suprascapula was present in *L. dynatis* it could not have been well developed, as its base of attachment was very thin. The triangular, posterolaterally facing supraglenoid buttress is well developed, with a vertically elongate, supraglenoid foramen near its dorsal apex. Although the scapulocoracoid is preserved occupying essentially a single plane, the coracoid plate undoubtedly had a pronounced ventromedial curvature approximating that of the clavicle. Williston (1911a) reported a suture between the anterior and posterior coracoids in *L. paludis*. This suture is not present in *L. dynatis*, but a broad, angular notch in the ventral margin of the coracoid plate





at approximately the same level may mark the junction of these two elements. The coracoid plate is smooth and appears to have been fairly thin at its anteroventral corner, where it would have underlain the clavicle and interclavicle. There is no tubercle for the coracoid head of the triceps. The long glenoid cavity is typical of most primitive tetrapods in being strongly screw-shaped, facing posterolaterally and slightly ventrally at its anterior end and dorsally at its posterior end. The glenoid extends to the posterior end of the dorsal margin of the coracoid plate (visible only in Fig. 11B of left element). The anterior end of the glenoid is supported strongly by the supraglenoid buttress dorsally and a laterally flared thickening of bone anteroventrally. Just behind the anteroventral thickening a deep fossa undercuts the anterior end of the glenoid, at the bottom of which probably lies the coracoid foramen.

*Forelimb.*—Elements of both forelimbs are represented except the left radius and both manus. The right humerus is essentially complete, and the left one is missing the proximal portion, but together they allow an accurate reconstruction (Fig. 12A). The short, stout humerus is very similar to that of *Limnoscelis paludis*. Noteworthy features in common include an extremely large, quadrangular entepicondyle, heavily built and strongly ossified supinator, pectoral, and deltoid processes, a platelike ridge extending along the dorsal surface from the ectepicondyle to the proximal articular surface, a platelike base of the supinator process, and a deeply hooked notch separating the supinator and deltoid processes.

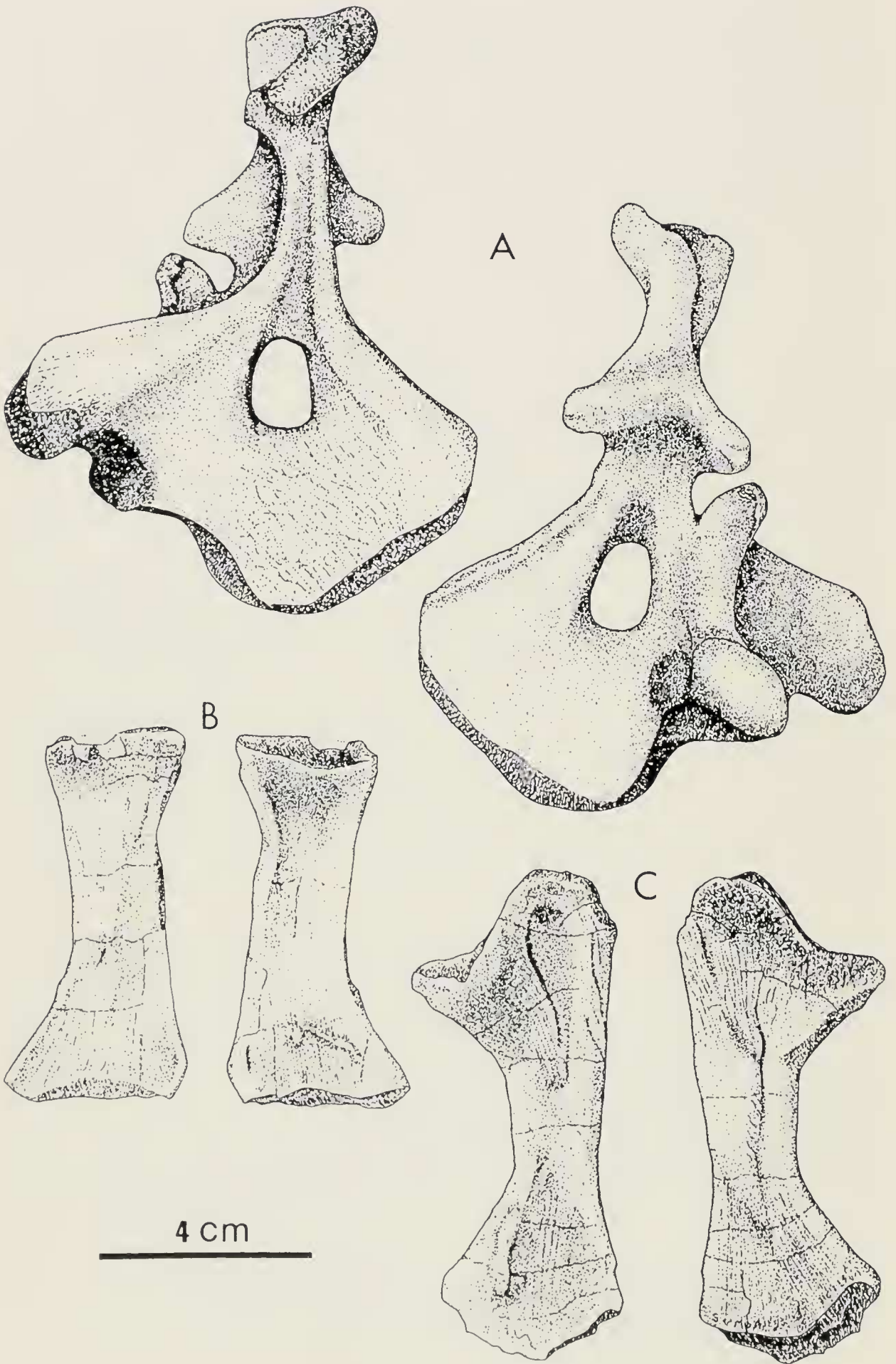
The radius (Fig. 12B) is slightly flattened dorsoventrally (=anteroposteriorly). The dorsal surface is somewhat convex with a blunt ridge running the length of the shaft, indicating that a substantial part of the extensor muscle mass for the manus originated from the radius. The ventral surface is slightly concave, especially near the proximal articulation. The proximal end is only slightly expanded over the shaft. Its articular surface, cupped to facilitate a sliding articulation with the rounded surface of the capitulum of the humerus, is semicircular with a strongly convex dorsal margin that reaches its greatest height near the lateral edge and a flattened ventral margin. The distal end of the radius is strongly expanded laterally. The flat, striplike distal articular surface is dorsoventrally narrower but mediolaterally wider than that of the proximal end, with the lateral edge being more pointed. A small right radius (6 cm long) is included in the paratype CM 47651.

Both ulnae (Fig. 12C) have undergone some dorsoventral compression. Although the olecranon is poorly developed and lacks obvious muscle scars, a heavy rugose ossification indicates a substantial attachment area for the triceps. A narrow strip of unfinished bone extends from the articular surface of the sigmoid notch over the apex of the low olecranon. The sigmoid notch widens dorsoventrally towards its medial margin, where it faces slightly dorsally. A low ridge extending the length of the ventral surface of the shaft marks the ulnar origin for the flexor musculature of the manus. The dorsoventrally narrow distal articular surface occupies the entire end of the bone and is divided into a slightly laterally facing area for the ulnare and pisiform and a slightly medially facing area for the intermedium of the carpus.

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Fig. 11.—*Limnoscelis dynatis*, holotype, CM 47653. Lateral views of A, right, and B, left scapulo-coracoids with partial left dentary in medial view adhering to left.





*Pelvis.*—The essentially complete, laterally exposed right pelvis (Fig. 13A) has suffered considerable fracturing and its sutures are indiscernible. However, study of the nearly complete, isolated left pubis and ischium allows an accurate reconstruction of the pelvis (Fig. 13B). The ilium has a well-developed posterior process and, although broken from the body of the ilium, appears to have extended almost directly posteriorly. The process ends, however, at a level far short of the posterior extent of the ischium. The distal half of the process exhibits coarse horizontal striae. There is little or no anterior expansion of the ilium. The ilium is proportionally very low and wide. The narrowest anteroposterior width of the neck of the ilium is slightly greater than the height of the ilium. A low, anteroposteriorly oriented but slightly wavy ridge extends across the upper half of the iliac blade, corresponding in its position to the external iliac shelf of *Diadectes*, *Seymouria*, and *Ophiacodon* (Romer and Price, 1940; Romer, 1956). The puboischiadic plate is long and nearly quadrangular. At the level of the midpoint of the acetabulum an angular notch in the ventral margin of the plate marks the union of the pubis and ischium. The pubis is vertically truncated anteriorly to form a right angle margin at its anteroventral corner. As a result, the pubis is roughly square in outline and is short compared to the ischium, occupying only 38% of the length of the puboischiadic plate.

The acetabulum is oval with its long axis directed anteroventrally. The iliac portion of the acetabulum is only weakly supported above by a ventrolaterally expanding buttress, whereas below it is strongly supported by a dorsolaterally expanding buttress of the puboischiadic plate. There is an extension of the anteroventral margin of the acetabulum as a narrow channel of unfinished bone that reaches the anterior margin of the pubis. The channel is not the result of preservational damage, as it is bounded dorsally and ventrally by liplike flanges, with that of the dorsal margin being particularly well developed and rugose. The channel is too narrow (6 mm) to have been part of the femoral articulation. An anteroposteriorly elongate obturator foramen exits through the pubis below the anteroventral margin of the acetabulum.

*Hindlimb.*—Elements of both hindlimbs are present except the pes. Both femora are nearly complete and lack much of the adductor crest, but the left one (Fig. 14A) is less distorted. The proximal and distal ends are widely expanded and joined by an extremely short and moderately stout shaft, giving the femur a deeply waisted appearance. The proximal head appears to be angled posteriorly when viewed dorsally or ventrally because its anterior border forms a nearly straight margin with the shaft and the posterior margin is strongly flared. The dorsal surface of the proximal head is moderately convex and smooth except for a prominent rugose area along its posterior margin that probably marks the site of insertions of the puboischiofemorales internus and ischiotrochantericus muscles. The proximal articular surface is crescentic, being slightly convex above and concave below, with the slightly channeled surface gradually narrowing posteriorly. The narrowly triangular, moderately deep intercondylar fossa deepens distally, turning sharply ventrally a very short distance from the end of the bone to

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Fig. 12.—Forelimb of *Limnoscelis dynatis*, holotype, CM 47653. A, dorsal and ventral views of reconstructed left humerus; B, dorsal and ventral views of right radius; C, dorsal and ventral views of left ulna.

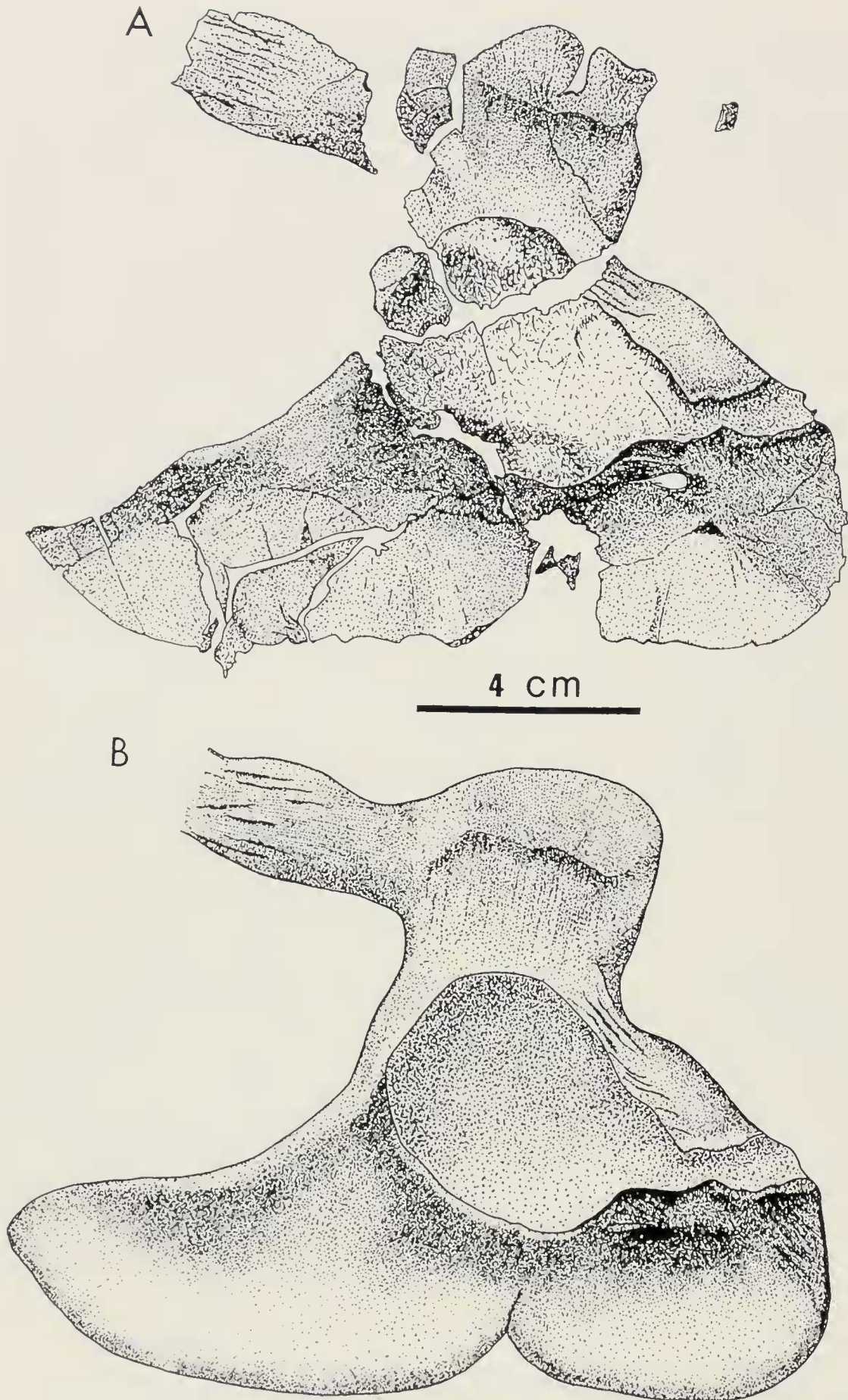


Fig. 13.—Lateral view of right pelvis of *Limnoscelis dynatis*, holotype, CM 47653. A, as preserved, and B, reconstructed.

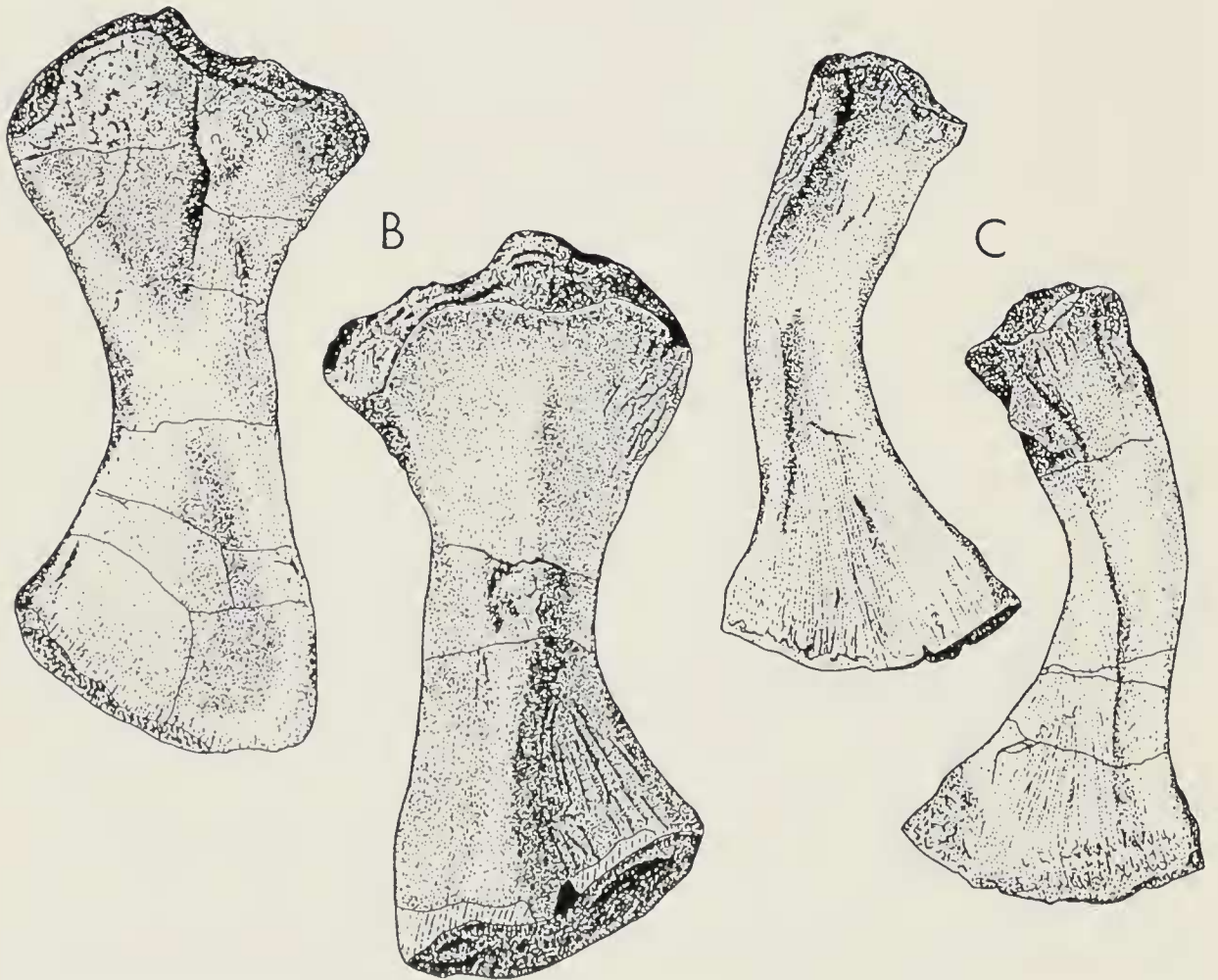
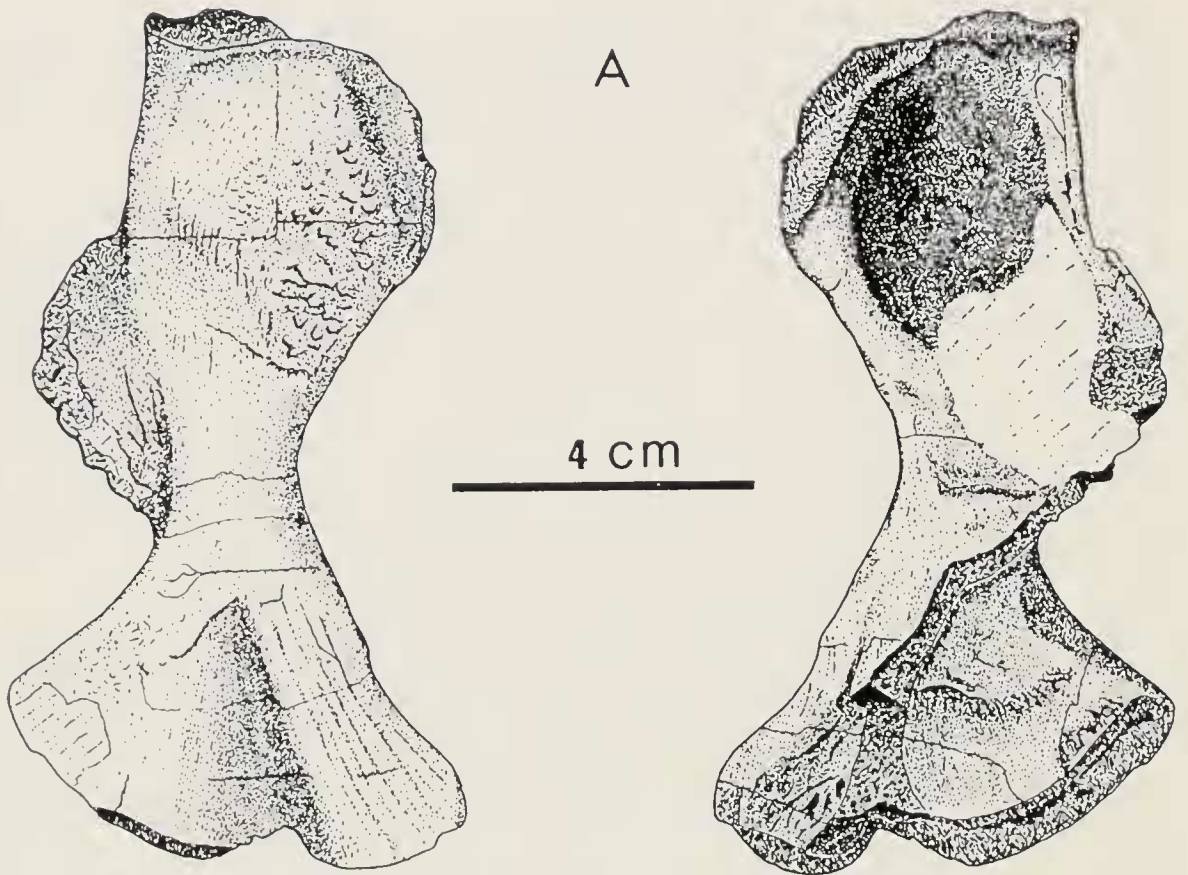


form a shallow intercondylar notch. The dorsal surfaces of the distal condyles are covered with minute proximodistal ridges that become coarser distally. The distal articular surfaces of the condyles are narrow, dorsally bowed strips in outline; that of the much narrower posterior condyle has a sharply angulated, almost chevron appearance.

Ventrally, about the proximal 40% of the femur is occupied by a very deep, oval intertrochanteric fossa. Although the adductor ridge is incomplete in both femora, it was well developed and extends distally from the anterodistal margin of the intertrochanteric fossa diagonally across the shaft. The region of the fourth trochanter at the proximal end of the adductor ridge is well developed in height and width, and its dorsal and ventral surfaces are coarsely rugose. An internal trochanter cannot be distinguished along the low anterior limiting ridge of the intertrochanteric fossa. Distally, the adductor ridge forms the posterior border of the deep popliteal fossa, occupying the ventral surface of the anterior condyle. The ridge terminates distally at a level along the ventral margin of the distal articular surface where the anterior and posterior condyles join.

The right tibia (Fig. 14B) is complete, whereas the left one is represented by only the proximal and distal ends. The tibia, though rather narrow dorsoventrally (=anteroposterior), is a mediolaterally broad, stout element with a short shaft. The lateral margin of the bone is more deeply concave than the medial margin, because the ends are much more strongly flared laterally. A prominent cnemial crest on the dorsal surface of the proximal head terminates proximally in a knob-like, rugose projection. Just lateral to the crest is a broad, shallow, triangular concavity. The proximal articular surface is gently sigmoidal in outline, with the medial end curved ventrally. The articular surface narrows steadily from a thick, bluntly rounded anterior end to a dorsally curving, pointed lateral end. The dorsal surface of the distal head is nearly flat, curving very slightly dorsally along its margin with the articular surface. A moderately elevated ridge runs almost the entire midventral length of the tibia. Midway along the ridge a very low protuberance may indicate where a portion of the tibialis posterior muscle originated. The distal articular surface is gently bowed dorsally, with the ventral convexity located more closely toward its posterior end. The tibia is about 16% longer than the fibula. The distal end of a right tibia of the same size as that of the holotype is included in the paratype CM 47652.

Both fibulae are complete and well preserved (Fig. 14C). Except for its proximal head, the fibula is strongly compressed dorsoventrally. At its narrowest point, the mediolateral width of the shaft exceeds the dorsoventral width by a little more than one-third. The dorsal surface of the proximal head is flat, and a proximodistally oriented channel (seen only on the figured right fibula) is undoubtedly due to crushing. The dorsal surface of the greatly expanded distal head is very slightly concave and is marked by very fine parallel striae. The slightly concave ventral surface of the proximal head actually faces ventromedially due to the great ventral thickening of the lateral portion. A thin, rounded, medially projecting flangelike process occurs within the concave depression a short distance from the proximal margin of the head. The ventral surface of the distal head is very slightly convex and, as on the dorsal surface, bears fine parallel striae. A very fine ridge extends the midventral length of the shaft. The proximal articular surface is slightly crescentic in outline, with the dorsal margin being very slightly convex and the ventrolateral margin greatly expanded so that the ventral concave margin actually faces ventromedially. The distal articular surface is a dorsoventrally very narrow strip that bows slightly ventrally and widens very gradually toward its medial end.





COMPARISONS WITH *LIMNOSCELIS PALUDIS*

In addition to *Limnoscelis paludis*, five other species in four genera of limnoscelids have been described from the Pennsylvanian and Permian, all based on extremely fragmentary specimens: *Limnosceloides dunkardensis* Romer (1952) from the Lower Permian Greene Formation of West Virginia; *Limnoscelops longifemur* Lewis and Vaughn (1965) from the Lower Permian Cutler Formation of Colorado; *Limnosceloides brachycoles* Langston (1966) from the Lower Permian Cutler Formation of New Mexico; *Limnostegis relictus* Carroll (1967) from the Middle Pennsylvanian Morien Group of Florence, Nova Scotia; *Romeriscus periallus* Baird and Carroll (1967) from the Lower Pennsylvanian of Nova Scotia. The close resemblance of *Limnoscelis dynatis* to *L. paludis* eliminates any possible doubt as to its generic assignment. Further, as far as can be determined, *L. dynatis* does not exhibit any shared derived characters that would suggest a closer relationship to a limnoscelid other than *L. paludis*. Yet, the two species differ in a significant number of characters.

Comparison of the cranial anatomies of *L. dynatis* and *L. paludis* is greatly facilitated by Fracasso's (1983, 1987) careful, comprehensive description of the holotypic skull of the latter. We have, however, also reexamined the holotypic skull of *L. paludis* and additional preparation has revealed some errors in his description which are noted below. Similar comparison of the postcranial skeletons of the two species is, however, not possible, given the incomplete and inadequate descriptions of *L. paludis* (Williston, 1911a, 1911b, 1912; Romer, 1946). This is due, in part, to the fact that most of the postcranial elements of the holotype and paratypes have never been fully exposed. For these reasons, only what appear to be obvious or marked differences in the postcranial skeleton are commented on here. Fortunately, the holotype of *L. dynatis* is about 20% smaller than the holotype of *L. paludis*, and differences between them are not likely to be due to different growth stages.

*Skull roofing bones.*—Of the preserved dermal roofing bones of the skull of *L. dynatis*, only the premaxillae and jugals differ substantially from that of *L. paludis*. The premaxilla in *L. dynatis* is not as massive, and in *L. paludis* the rostral body of the premaxilla is more greatly developed anteroposteriorly, so that the premaxilla, and not the maxilla as in *L. dynatis*, forms almost the entire ventral border of the external naris. Unlike *L. paludis*, the dorsal processes of the premaxillae of *L. dynatis* did not enclose an internasal on the midline. The jugal in *L. paludis* has no postorbital process or bar, the contact with the squamosal is weakly serrate and nearly straight, and the free edge along the ventral margin of the skull is broadly concave so as to produce a narrower posterior extension. In *L. dynatis*, on the other hand, the jugal has a well-developed postorbital process or bar, a smooth, broadly concave, external line of contact with the squamosal, and a straight free edge along the ventral margin of the skull that results in a much broader posterior extension.

*Palate.*—In the palate of *L. paludis*, the transverse flange of the pterygoid is a straight, posterolaterally oriented, toothed ridge. The width of the toothed ridge is constant and supports a single row of five or six teeth which range in size from

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Fig. 14.—Hindlimb of *Limnoscelis dynatis*, holotype, CM 47653. A, dorsal and ventral views of left femur; B, dorsal and ventral views of right tibia; C, dorsal and ventral views of right fibula.

2 to 6 mm in basal diameter, decrease in size toward the lateral end of the ridge, and exhibit infolding. In contrast, the toothed transverse flange in *L. dynatis* is narrowly subtriangular with the laterally directed apex curving slightly posterolaterally. The toothed ridge is covered by densely packed, blunt denticles ranging in diameter from 0.3 to 0.8 mm except for a single row of as many as eight larger teeth (diameter = 2 mm) along the posterior margin of the ridge. None of the teeth exhibit infolding.

Fracasso (1983, 1987) described the vomer of *L. paludis* as having as its anterior end an unusual lateral, winglike structure that consists of a broad, rectangular plate closely apposed to the internal subnarial and postnarial walls of the snout and forms the anterolateral border of the internal naris. This sort of structure is, as far as we are aware, unique among Paleozoic tetrapods. Our examination of the holotype of *L. paludis* reveals no evidence that would confirm or refute the presence of a lateral winglike process of the vomer, but two features of its skull may have misled Fracasso to interpret the existence of this odd structure of the vomer: 1) the typical narrow contacts between the vomerine processes of the premaxillae and the anterior ends of the vomers that are restricted to the area between the internal nares are not detectable most likely because of poor preservation; and 2) what appears to be the distal ends of the processes in Fracasso's description are more likely the maxillary processes of the premaxillae that have been displaced slightly medially from their maxillary contact. In *L. dynatis* the suture on the premaxilla for the vomer is limited to a small vomerine flange that extends posteriorly from the ventral half of the posteromedial margin of the rostral block. Further, the medial surface of the maxillary process of the premaxilla is smooth and undoubtedly formed the anterolateral border of the internal naris.

*Marginal dentitions.* — The first and largest of the premaxillary teeth in *L. paludis* (greatest basal diameter = 14 to 15 mm; length = 40 to 45 mm) is considerably larger relatively than that of *L. dynatis* (diameter = 10 mm; length = 26 mm), in which the smaller size probably reflects the less massive size of the rostral body of the premaxilla. The estimated maxillary tooth count of 17 to 20 for *L. paludis* is less than the 22 to 23 of *L. dynatis*. In the dentary *L. paludis* has an estimated 15 to 18 teeth and *L. dynatis* 23 or 24. Though the second tooth in both series is the largest, it is larger in *L. paludis* (greatest diameter = 14 to 15 mm and length = 33 to 39 mm, versus 11 and 30 mm, respectively, in *L. dynatis*). The magnitude of this difference cannot be accounted for by the smaller size of *L. dynatis*. The remainder of the dentary teeth in both species are comparable in size except for the first, which in *L. paludis* is about half as large as the second, but in *L. dynatis* is nearly as large, with a greatest diameter of 10 mm and a length of 23 mm.

*Braincase.* — The braincases of both species are very similar; however, errors in Fracasso's (1983, 1987) description of the occiput of *L. paludis*, due in great part to inadequate preparation, falsely indicate noteworthy differences. In order to prevent confusion it is necessary to briefly note the more important mistakes in Fracasso's description. The exoccipitals of *L. paludis* are not, as Fracasso illustrated, small triangular elements restricted to the lateral margins of the foramen magnum, but are much larger and also include indeterminable dorsolateral portions of the occipital condyle that meet or almost meet on the floor of the foramen. Fracasso shows erroneously the supraoccipital-opisthotic suture as extending dorsolaterally at about a 45° angle from the ventral margin of the small triangular exoccipital at about the ventrolateral level of the foramen magnum.



This reconstruction not only depicts the dorsal triangular portions of the exoccipital as articulating anteriorly mainly with the supraoccipital, but the supraoccipital as forming most of the lateral walls of the foramen magnum anterior to the exoccipitals. What Fracasso identified as the supraoccipital-opisthotic sutures are nearly symmetrical fractures. The true sutures can be found with difficulty as extending dorsally for a short distance from the dorsolateral margin of the foramen magnum, then angling dorsolaterally at about 30° from the horizontal to the margin of the occiput. This reinterpretation duplicates the pattern in *L. dynatis*, where the supraoccipital forms only the dorsal margin of the foramen magnum and the dorsal processes of the exoccipitals form the lateral margins, thus articulating anteriorly with the opisthotics. Fracasso (1987) does not identify a jugular foramen and mistakes an extremely small pocket of matrix on the ventral end of the small triangular dorsal portion of the left exoccipital as the foramen for the hypoglossal nerve. Further preparation has located both these foramina in their normal positions, the hypoglossal foramen on the lateral surface of the neck of the occipital condyle and the jugular foramen anterior to it on the exoccipital-opisthotic suture. Fracasso (1987:9) was unable to locate the suture between the opisthotic and the basioccipital-exoccipital complex and mistakenly described the otic trough as appearing “to be continuous with the basioccipital in *Limnoscelis*, as there is no evidence of sutures or other separation between the trough bases and the basioccipital.” Examination of the holotype of *L. paludis* reveals this suture to be present in its standard position between the otic trough and basioccipital-exoccipital complex. Removal of residual matrix also reveals that the notch between the paroccipital process and otic trough is much deeper and more sharply V-shaped in *L. paludis* than indicated by Fracasso.

*Appendicular skeleton.*—The scapulocoracoids of *L. paludis* and *L. dynatis* differ in the relative height of the blade. Judging from Williston’s (1911*a*, 1911*b*; 1912) description of *L. paludis*, the height of the blade measured from the dorsal margin of the glenoid exceeds by a third its greatest anteroposterior width near the summit. In *L. dynatis* the greatest width of the blade only slightly exceeds its vertical height. Unlike *L. dynatis*, *L. paludis* lacks an angular notch in the ventral margin of the coracoid plate. Romer’s (1946) reconstruction of the pelvis of *L. paludis* differs significantly from the pelvis in *L. dynatis*. In *L. paludis* the vertical height of the blade measured from the dorsal margin of the acetabulum exceeds its narrowest anteroposterior width across the neck by at least 70%. In contrast, the ilium of *L. dynatis* is very low and wide, and the narrowest width slightly exceeds the height. Whereas the posterior process of the ilium of *L. paludis* extends to a level equal to that of the posterior end of the ischium, that of *L. dynatis* terminates at a level far shorter. The pubis of *L. paludis* is typical of amniotes in extending anteriorly to form an acute angle at its anteroventral corner and occupying about 46% of the puboischiadic plate length. The pubis of *L. dynatis* ends anteriorly in a vertically truncated margin, giving it a roughly square outline and shortening its anteroposterior length to only about 38% of the puboischiadic plate length. In these features, the pubis of *L. dynatis* resembles that of certain primitive anthracosaurs such as *Archeria* and *Proterogyrinus* (Holmes, 1984). In *L. paludis* the external iliac ridge forms a pocket bounded laterally by a thin, vertical flange of bone, whereas in *L. dynatis* the ridge is low. In both species there is an unusual channellike anteroventral extension of the acetabulum. The channel in *L. paludis*, however, is abbreviated to a tongue-like projection that is only half as long as that of *L. dynatis*, which reaches the anterior margin of the pubis.

In *L. paludis* the fibula is slightly longer than the tibia, whereas in *L. dynatis* the tibia is about 16% longer than the fibula.

The polarities of many of these characters can be determined with reasonable certainty using Seymouriamorpha (*Seymouria*) and primitive anthracosaurs (*Anthracosaurus*, *Archeria*, *Eoherpeton*, and *Proterogyrinus*) for comparison, as these taxa have been recognized most recently as the primitive reference outgroups for diadectomorphs (Gauthier et al., 1989; Panchen and Smithson, 1989). Those characters indicating that *L. paludis* is derived relative to *L. dynatis* include: 1) rostral body of premaxilla is more massively developed and forms almost the entire ventral border of the external naris; 2) an internasal bone is present; 3) the free edge of the jugal along the ventral margin of skull is broadly concave, giving its posterior extension a narrower attenuated appearance; 4) transverse flange of pterygoid is narrow and straight, and its single row of teeth are larger; 5) fewer and generally larger marginal teeth; 6) greater development of the external iliac shelf; and 7) pubis extends farther anteriorly, tapering to an acute angle at its anteroventral corner, and accounts for nearly half the length of the puboischiadic plate.

On the other hand, far fewer characters suggest that *L. dynatis* is more derived: 1) jugal possesses a postorbital bar and has a broadly concave external line of contact with the squamosal; 2) the anteroventral channellike extension of the acetabulum is about twice as long and reaches the anterior margin of the pubis. Thus, on balance, it seems that *L. paludis* is much more derived relative to *L. dynatis*.

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